BULLETIN

OF THE

TORREY BOTANICAL CLUB

VOL. 43

FOUNDED BY WILLIAM HENRY LEGGETT, 1870

EDITOR

ALEXANDER WILLIAM EVANS

ASSOCIATE EDITORS

JEAN BROADHURST
JAMES ARTHUR HARRIS
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HERBERT MAULE RICHARDS
ARLOW BURDETTE STOUT
NORMAN TAYLOR

NEW YORK
1916
PUBLISHED FOR THE CLUB
THE NEW ERA PRINTING COMPANY
LANCASTER, PENNSYLVANIA

VOL. 43 JANUARY 1916 NO. 1

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PUBLISHED FOR THE CLUB

THE NEW ERA PRINTING COMPANY
LANCASTER, PA.

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All subscriptions and other business communications relating to the publications of the Club should be addressed to the Treasurer, Dr. Bernard O. Dodge, Dept. of Botany, Columbia University, New York City.

Bulletin. Monthly, established 1870. Price, $3.00 a year; single numbers 30 cents. Of former volumes, only 24–39 can be supplied separately; certain numbers of other volumes are available, but the entire stock of some numbers has been reserved for the completion of sets. Manuscripts intended for publication in the BULLETIN should be addressed to the Editor, Osborn Botanical Laboratory, Yale University, New Haven, Connecticut.

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Covers: 25 for 75 cents, additional covers 1 cent each.

Plates for reprints, 40 cents each per 100.

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Dates of Publication

No. 1, for January.	Pages 1– 62.	Issued February 15, 1916.
No. 2, for February.	63–116.	March 11, 1916.
No. 3, for March.	117–168.	April 14, 1916.
No. 4, for April.	169–206.	May 20, 1916.
No. 5, for May.	207–282.	June 16, 1916.
No. 6, for June.	283–342.	June 29, 1916.
No. 7, for July.	343–396.	August 14, 1916.
No. 8, for August.	397–440.	August 22, 1916.
No. 9, for September.	441–504.	October 20, 1916.
No. 10, for October.	505–544.	November 7, 1916.
No. 11, for November.	545–600.	November 27, 1916.
No. 12, for December.	601–676.	January 6, 1917.

Errata

Page 92, line 2 from bottom, omit "about half natural size."
Page 345, lines 15–22, omit all species of *Potamogeton* and *Triglochin*, except *P. alpinus*.

Vol. 43 No. 1

BULLETIN

OF THE

TORREY BOTANICAL CLUB

JANUARY, 1916

Physiological observations on Drosera rotundifolia *

HENRY D. HOOKER, JR.

(WITH ELEVEN TEXT FIGURES)

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1. INTRODUCTION

The object of the work, which this paper presents, was to determine whether the bending of *Drosera* tentacles was connected with a temporary acceleration of the rate of growth or with differences of turgidity; in physiological terms, whether the bend-

* Contribution from the Osborn Botanical Laboratory.

[The BULLETIN for December (42: 651–698. *pl. 30–33*) was issued January 20, 1916.]

ing was a nutation or a variation movement. Analogy with the behavior of tendrils, which has been thoroughly investigated by Fitting, indicates that the reactions of *Drosera* are phenomena of growth, and this is substantiated by Batalin's ('77, p. 36) somewhat meager measurements. These are, in Pfeffer's words ('06, 3: 85), "not fully satisfactory." Although the primary purpose of this paper is to settle this point, a number of observations were made during the work which pertain to other matters. These minor points are of some physiological interest and will be mentioned before proceeding to the main discussion.

2. MATERIAL

The material used was collected during the months of July and August from Beaver Swamp in the city of New Haven, Connecticut. It was found advisable to use only fresh material for experimentation.

Plants of *Drosera rotundifolia* and *D. longifolia* were found growing in *Sphagnum*. In removing them, large pieces of the substratum were taken along with the plants to prevent injury to the roots and to insure their further development in the laboratory. Slight injuries to the roots cause the secretion of the glands to stop and render the tentacles inactive, so that they fail to respond to the customary stimuli. The root-hairs are particularly remarkable, for they are not restricted to a small region above the root-tip but cover the entire length of the root. They do not die, but continue to grow and function. In this way they increase the effectiveness of the small root-system.

The plants were placed in flat dishes, made wet with distilled water and covered with bell-jars. Under these conditions the development of the plants was far from normal. The rosette arrangement of the leaves was lost, a typical stem was developed by lengthening of the internodes and every trace of red pigment disappeared. No gradations from purple to green leaves were observed. All the leaves, which unfolded in the moist atmosphere and subdued light of the culture, were green. The size of the leaves diminished and their petioles made a more acute angle with the stem, causing them to point obliquely upward instead of horizontally outward.

3. PIGMENT

The red pigment of *Drosera* occurs predominantly in the leaves and the root-cap. Young leaves frequently have the pigment restricted to the glands of the tentacles. Later it appears in the epidermal cells of the marginal pedicels. Leaves of old plants often have the entire leaf-blade pigmented and, as the leaf matures, the color spreads down the petiole and often into the stalk. In general young plants are much greener than old ones, but wide variations are found.

The red pigment of *Drosera rotundifolia* and *D. longifolia* is identical with one of the pigments which Rennie ('87, '93) extracted from rhizomes of *D. Whittakeri*. Its formula is $C_{11}H_8O_5$, and it is probably trihydroxymethylnapthoquinone, since it gives the reaction of Brissemoret and Combes ('07) characteristic of α-napthoquinones.

To obtain the pigment, place a deep red leaf on a slide, add a few drops of hot alcohol, put on a cover-glass and heat directly over boiling water. The pigment is extracted from the leaf and, on the evaporation of the alcohol, it is deposited around the edges of the cover-glass. It forms crystals which are small red disks. It is insoluble in cold water, hardly soluble in cold alcohol and glacial acetic acid, but dissolves readily in boiling water, hot alcohol and ether, and to a lesser extent in benzol and carbon disulphide. It is soluble in alkalis. When a leaf is treated with ammonia, the pigment turns dark violet or brown; on standing the color fades. A timely treatment with dilute acid precipitates the pigment and restores the red color, but this does not occur after prolonged action of the ammonia. Reduction with stannous chloride and alcoholic hydrochloric acid gives a yellow product which crystallizes in needles. This is reoxidized to the original compound, when allowed to stand in alcoholic or alkaline solution exposed to the air. These properties were found for the pigment of *D. rotundifolia*. They coincide with those given by Rennie for the compound $C_{11}H_8O_5$, and confirm the suggestion of their identity put forward by Kraemer ('10, p. 285).

Experiments were made with the green plants to determine under what circumstances the pigment reappeared. Several plants of *D. longifolia* were cultivated for a month in a moist

atmosphere, without being fed with insects. They lost all traces of pigment. Six of these were fed with small flies and two days later pigment was observed in the marginal tentacles of the youngest leaves, that had just unrolled. A similar reappearance of color was observed in three other plants which caught insects. This is the opposite of the results obtained by F. Darwin ('08, p. 23) and by Büsgen ('83, p. 592), who found that plants fed with insects had much greener leaves than those which relied solely on photosynthesis for their nourishment. The contradiction may be owing to different environmental conditions, such as the chemical composition of the substrate, the intensity of the light, or the humidity of the atmosphere. The question merits further investigation.

4. HABIT

Another peculiarity observed in plants cultivated in a moist atmosphere was the peculiar habit assumed by the plant. The internodes became lengthened, and this was the case with plants exposed either to the diffuse light of the laboratory or to direct sunlight. Plants exposed to dry air were observed to retain the rosette habit under both light conditions. This shows that the rosette habit characteristic of *D. rotundifolia* is dependent upon transpiration and not upon light, as Diels ('06, p. 32) suggests. This relation represents an interesting adaptation, for as long as the plant is beneath the surface, the internodes lengthen, since transpiration is reduced to a minimum. In this way the terminal bud is brought to the surface, where rapid transpiration from the exposed leaves causes the development of a rosette.

5. PARASITES

A great many of the plants cultivated in the laboratory were destroyed by larvae accidentally brought with the material from the swamp. They were larvae of one of the cut-leaf moths or noctuids. Since the adult form has not been obtained, it has been as yet impossible to identify them. The young larvae are about a quarter of an inch long and very pale. They climb up the under side of the leaf-petioles and eat the blade from behind. In this way they avoid the tentacles which could easily catch and digest such small creatures. The larvae select the youngest

leaves and destroy the plant by eating the terminal bud. Many of the fragments of partially eaten leaves fall onto the *Sphagnum* and produce new plants by regeneration. Here again is an arrangement which may be considered a reciprocal adaptation; the larvae are protected from the leaves which could consume them, and the destruction of the plant by the larvae results in vegetative reproduction. As the larvae grow older they increase greatly in size and become green. Even after they have reached a size which renders their capture by a *Drosera* leaf impossible, they continue to crawl along the under surface and eat the leaves from behind. They become exceedingly voracious and a single insect can devour a dozen flourishing plants in two days.

6. Cultivation

The *Drosera* plants used for experimentation were grown in uncovered dishes exposed for at least six hours a day to direct sunlight. Small flies and other insects were placed on the leaves from time to time. The best leaves were selected for reactions and were not fed. In one remarkable instance, a house-fly was placed on a small fresh leaf which was only slightly pigmented. A copious secretion resulted which enveloped and digested the fly. After five days, however, the entire leaf-blade had disappeared, being digested by its own fluid. The plant was not vigorous and the fly was too large for the leaf, but normally anti-enzymes or other adequate means must be present to prevent autolysis.

7. Mechanics of Movement

(*a*) Normal Development

The blade of the undeveloped *Drosera* leaf is rolled up. As it expands the marginal tentacles are seen to be bent over the blade, the glands pointing against the leaf and the pedicels arranged like rays around the edge. As the leaf grows, these tentacles increase considerably in length, the growth being greater on the adaxial side. By this means the incurved tentacles are straightened, a process which is assisted by the simultaneous flattening of the leaf-blade. When all the tentacles are straight, the leaf is mature and able to catch insects. The full grown tentacles do not increase perceptibly in length. They remain in this condition for about

two weeks, during which time their glands secrete actively. At the end of this period the tentacle begins to bend backward. In old leaves the marginal tentacles are much recurved, and in extreme cases the gland may pass through a complete revolution by the rolling up of the distal portion of the pedicel. The petiole of young leaves points up. As the leaf ages, its petiole bends down so that the mature leaf is horizontal.

The pedicels of the exterior tentacles are dorsi-ventrally flattened at the base. The abaxial side has numerous short glandular hairs distributed over its entire length. On the adaxial side they are fewer in number and are confined more or less to the base.

(*b*) EXPERIMENTAL METHOD

Fresh leaves which had not been previously touched were selected for experimentation. The entire plant was removed from the *Sphagnum* in which it grew and was placed in a large Stender dish. A piece of cork was fastened with sealing wax inside the dish and another piece attached to it by two pins. The petiole of the selected leaf was clamped horizontally between the two pieces of cork in such a way that the leaf-blade was vertical. The bottom of the dish was covered with water and the roots were wrapped in wet sphagnum. The cover of the Stender dish was replaced or discarded, as desired. A binocular microscope was used, because the greater distance from the objective to the object made it more convenient when the Stender dish was covered. An horizontal tentacle, which showed glandular hairs on both upper and lower sides and which was not obscured by its neighbors, was selected from the edge of the leaf opposite the petiole. Its pedicel was marked with China ink to facilitate identification.

Each tentacle was measured with a micrometer scale and drawn with a camera lucida before an experiment. The gland was then stimulated by placing upon it some object such as the leg of a fly. This was removed as soon as movement began. At each subsequent observation the time was recorded and the tentacle was sketched. This was continued at intervals until the pedicel was again straight. The tentacle was then measured for the second time with the micrometer scale.

The figures given in the tables are in hundredths of a millimeter. Measurements were made on the drawings, which were checked by the direct measurements. The time at the head of the first column shows when the gland was stimulated. The column to the right of the heavy line shows the first indication of unbending. The segments were marked off naturally by the presence of glandular hairs on the two flattened surfaces. They are numbered from the apex to the base. The segments on the concave side do not always correspond to those on the convex side.

TABLE I

	No. of Segment	10.00 A. M.	10.15 A. M.	10.35 A. M.	11.00 A. M.	11.20 A. M.	11.40 A. M.	12.00 M.	1.15 P. M.	2.00 P. M.	3.00 P. M.	3.30 P.M.	4.00 P. M.	4.30 P. M.	5.00 P. M.	7.35 P. M.	9.00 P. M.	9.10 P. M.
Abaxial side	1	80	80	80	80	80	80	80	80	80	80	80	80	80	80	80	80	80
	2	23	23	23	23	23	25	25	25	25	25	25	25	25	25	25	25	25
	3	24	25	25	25	28	28	28	28	28	28	28	28	28	28	28	28	28
	4	29	31	31	32	34	35	35	35	35	35	35	35	35	35	34	34	34
	5	36	41	41	42	43	45	49	49	49	48	48	48	48	48	48	48	46
	6	43	51	52	53	55	57	59	59	59	59	58	57	55	55	55	55	55
	7	59	60	60	60	61	69	70	72	72	72	71	69	69	69	69	69	69
	Total..	294	311	312	315	324	339	346	348	348	347	345	342	340	340	339	339	337
Adaxial side	1	78	78	78	78	78	78	78	78	78	78	78	78	78	78	78	78	78
	2	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	24
	3	24	25	25	25	25	25	25	25	25	25	25	25	26	26	26	27	27
	4	31	31	31	29	29	29	28	28	28	29	29	29	29	31	32	33	34
	5	40	40	40	40	40	40	40	40	41	41	41	41	41	41	43	44	46
	6	28	29	29	29	31	32	32	32	34	35	35	35	35	35	35	36	38
	7	28	28	28	28	28	28	28	28	28	29	31	32	33	34	34	35	37
	8	45	45	45	45	46	48	49	50	50	50	50	50	50	51	51	52	54
	Total..	297	299	299	297	300	303	303	304	307	310	312	313	315	319	322	328	338

(*c*) EXPERIMENTAL DATA

Measurements of the dorsal and ventral sides of a tentacle in the process of bending and unbending are given in TABLE I. The tentacle was selected from next to the outermost row on a fresh, red, young leaf which was secreting copiously. The leaf had been protected during its development and was not touched, or stimulated in any other way, prior to the experiment. Its reaction is typical of the marginal tentacles on young leaves, unless perhaps it is more than usually vigorous.

The straight tentacle measured 2.94 mm. in length. The leg of a small house-fly was laid on the gland. One minute and a

half after stimulation movement was detected, whereupon the fly-leg was removed. After fifteen minutes the tentacle was well bent and the gland had moved through an angle of about fifty degrees. Marked elongation took place on the convex side near the base in Segment 6, and to a lesser extent in Segment 5. The concave side remained nearly of the same length as before. The region of bending is coincident with the region of elongation on the

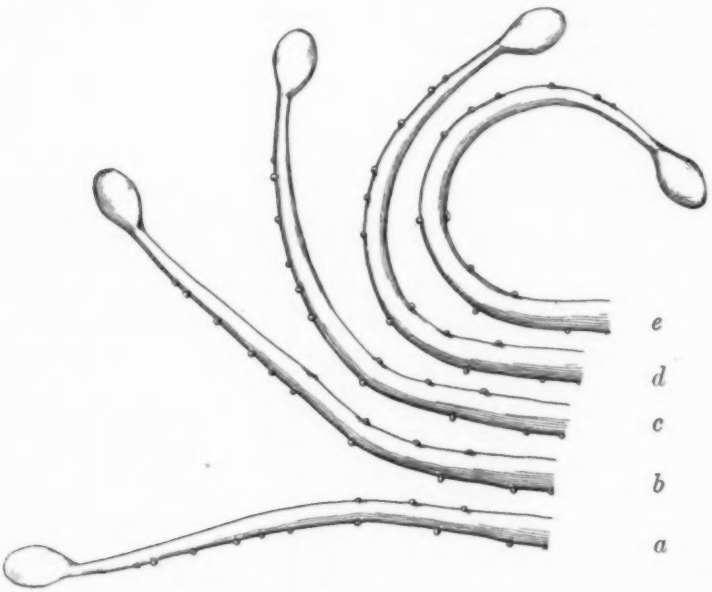

FIG. 1. Side views of a tentacle in the process of bending, × 22. *a*, before stimulation; *b*, *c* and *d*, successive stages of inflexion; *e*, the fully bent tentacle.

convex side. As the tentacle continued to bend, the area of curvature and elongation was extended upward toward the gland, including Segments 4, 3, and 2, and to a lesser extent downward so as to include a portion of Segment 7. In the ultimate stage the curved region subtended an angle of approximately 215 degrees. Both sides increased in length, but the increase of the convex side was eight times that of the concave. FIG. 1 is a series of camera lucida drawings made during the inflexion of this tentacle. In *b* the bending region is seen to be restricted at first to the lower end and to extend apically in *c* and *d*. The final

condition attained 3 hours and 15 minutes after stimulation is shown in *e*.

Unbending commenced immediately. TABLE I shows that this resulted from elongation of the concave side and contraction of the convex side. The region of elongation is at first near the base in Segment 7, which lies opposite the lower portion of Segment 6 on the convex side. This region gradually extends apically. The contraction on the convex side is mostly confined to the base, and it is moreover relatively slight, being only one fourth the amount of elongation on the concave side. FIG. 2 shows the result of these alterations in length. Since the reaction commences near the base, this portion is the first to straighten;

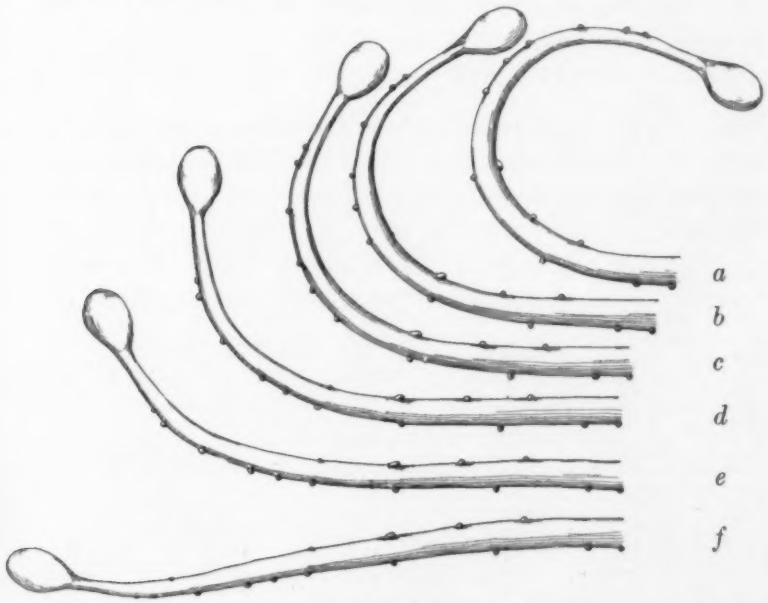

FIG. 2. Side views of the tentacle shown in FIG. 1 in the process of unbending. × 22. *a–e*, successive stage in the expansion; *f*, the tentacle at the completion of the reaction.

as successive portions on the concave side further removed from the base elongate, the straight part of the pedicel lengthens. In unbending the tentacle is therefore curved in a different manner than during bending. In the latter case, the principal curve is near the base, in the former, nearer the apex. A comparison of

FIG. 1, *a* and *b*, with FIG. 2, *d* and *e*, illustrates this. The most apical part which elongated during the process of bending is the last to regain its original position. The basal portion, however, does not stop increasing its length until the entire tentacle is straight. At the end of the reaction, after 23 hours and 10 minutes, the tentacle measured 3.37 mm. It had therefore *grown* during the process of bending and unbending 0.43 mm. (See

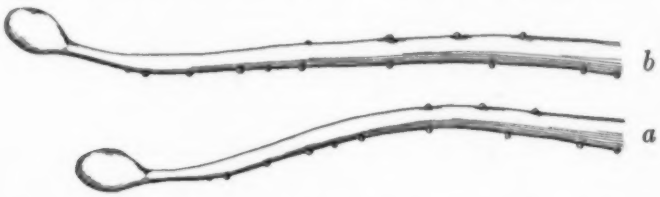

FIG. 3. Side views of the same tentacle before and after the reaction, to show the increase in length, × 22. *a* is the same as FIG. 1, *a*; *b* is the same as FIG. 2, *f*.

FIG. 3). A control tentacle which had not been stimulated measured before and after the experiment 2.57 mm. Another measured 2.6 mm. They had not grown a measurable amount during the interval.

FIG. 4 is a graphical representation of the growth of the tentacle. The elongation of the abaxial side is shown by the

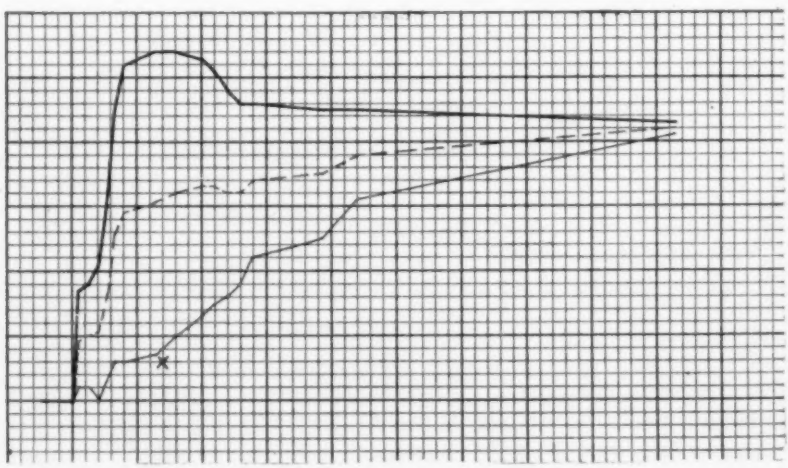

FIG. 4. A graph representing the reaction shown in FIGS. 1 and 2, drawn according to data in TABLE I. See text for explanation.

heavy line; the growth of the adaxial side is shown by the light line. The calculated growth of the median section of the tentacle is given by the broken line. The time is plotted on the abscissae; each space is thirty minutes. The changes in length are plotted on the ordinates; each space represents 0.02 mm. The reaction time is not indicated. The cross shows when the bending was completed and when unbending began. It is evident from the figure that the inflexion of the tentacle is produced by a considerable acceleration of the rate of growth on the abaxial side and in the median section. The unbending is more gradual and takes six times as long as the bending. Moreover the unbending is produced by a similar but less intense acceleration of the growth on the adaxial side and in the median section together with contraction of the abaxial side during the beginning of the process.

The reaction of another tentacle is shown in TABLE II and FIG.

TABLE II

	No. of Segment	10.16 A. M.	10.54 A. M.	11.18 A. M.	11.28 A. M.	11.31 A. M.	11.36 A. M.	12.09 P. M.	12.38 P. M.	3.58 P. M.	9.45 A. M.
Abaxial side	1	72	72	72	72	72	72	72	72	72	72
	2	118	118	118	118	118	118	119	119	119	119
	3	26	27	28	28	31	32	33	34	36	34
	4	54	54	54	58	58	58	58	59	59	58
	Total	270	271	272	276	279	280	282	284	286	283
Adaxial side	1	72	72	72	72	72	72	72	72	72	72
	2	121	121	121	121	121	121	120	120	120	121
	3	35	35	35	35	35	35	35	34	33	43
	4	38	37	37	37	36	35	35	34	34	42
	Total	266	265	265	265	264	263	262	260	259	278

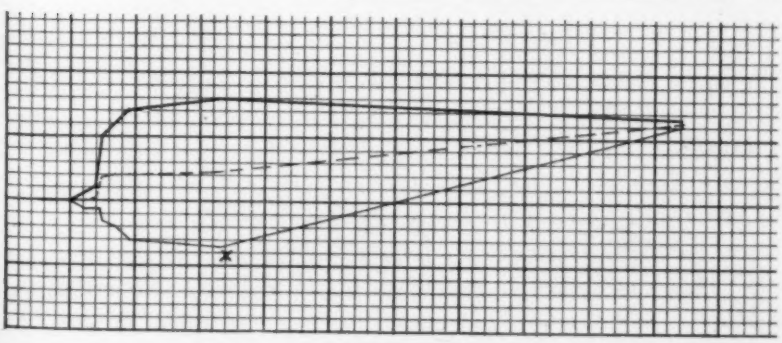

FIG. 5. A graph representing the bending and unbending of a tentacle, drawn according to data in TABLE II, and on the same scale as FIG. 4.

5. Before the experiment it measured 2.7 mm. The reaction is in all essential respects similar to the previous example, but there are important differences. The tentacle was on a mature leaf. It had not, however, been stimulated before the experiment. Bending was produced by an elongation of the convex side and the median section, accompanied by contraction of the concave side. The increase in length on the abaxial side was twice as great as the contraction of the adaxial side. The ultimate stage of bending was reached 5 hours and 45 minutes after stimulation. Unbending was caused by gradual growth on the concave side and in the median section together with slight contraction of the convex side. The original position was reached after 23 hours and 30 minutes. The tentacle then measured 2.83 mm. It had grown 0.13 mm. during the experiment.

A third example is given in TABLE III. This tentacle was in

TABLE III

	No. of Segment	3.45 P. M.	3.52 P. M.	3.55 P. M.	3.58 P. M.	4.01 P. M.	4.05 P. M.	9.20 A. M.	4.00 P. M.	9.00 A. M.
Abaxial side	1	84	84	84	84	84	84	84	84	84
	2	57	57	58	58	58	58	58	58	58
	3	37	37	37	37	40	41	42	43	43
	4	31	31	31	34	40	43	43	43	43
	5	45	47	52	53	57	57	54	50	49
	Total...	254	256	263	266	279	283	281	278	277
Adaxial side	1	82	82	82	82	82	82	82	82	82
	2	57	57	57	57	57	57	58	59	61
	3	58	58	58	58	59	59	60	62	66
	4	46	46	42	37	37	40	42	42	42
	5	12	12	12	12	12	12	23	23	24
	Total...	255	255	251	246	247	250	265	268	275

the third row from the outside, on a leaf in excellent condition. It reacted with great rapidity. Movement was detected within a minute after stimulation, and the bending was completed in twenty minutes. The table shows clearly that elongation commenced in Segment 5, the most basal portion of the abaxial side; after ten minutes Segment 4 likewise increased in length; and after three minutes more Segment 3 began to grow. The drawings in FIG. 6 show the bending, and illustrate the apical progress of the reaction. As in the previous case, the bending was produced

by acceleration of the growth on the convex side and in the median section, with contraction of the concave side.

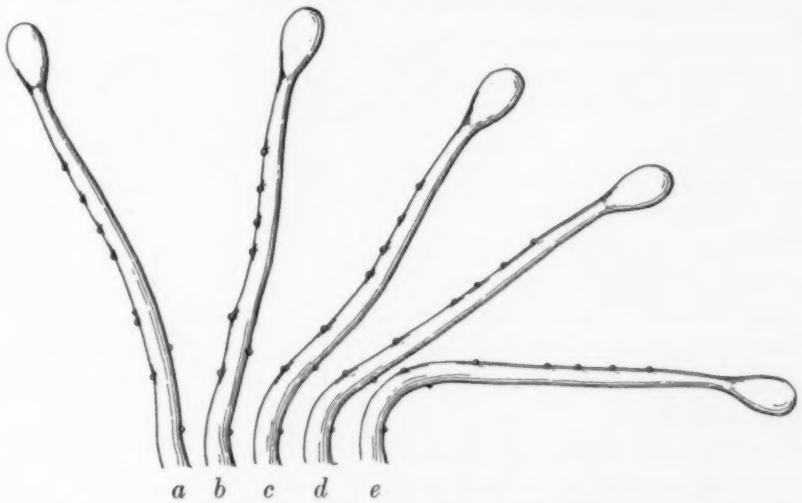

FIG. 6. Side views of a tentacle in the process of bending. × 22. *a*, the straight tentacle before stimulation; *e*, the inflected tentacle twenty minutes after stimulation.

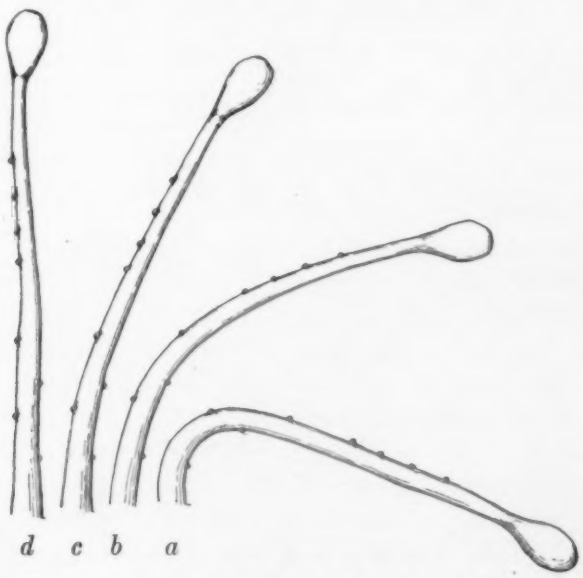

FIG. 7. Side views of the tentacle shown in FIG. 6 in the process of unbending. × 22. *a*, the fully inflected tentacle; *d*, the straight tentacle at the end of the reaction.

The unbending presents no new features. FIG. 7 shows successive stages in the process and comparison with FIG. 6 emphasizes the different configuration of the bending and unbending tentacle. The tentacle grew from 2.54 mm. to 2.77 mm., an increase of 0.23 mm.

The reaction is plotted in FIG. 8. The complete reaction took 39 hours and 15 minutes, an unusually long time. This experiment is perhaps more representative than the first in that growth was confined to the lower half of the pedicel.

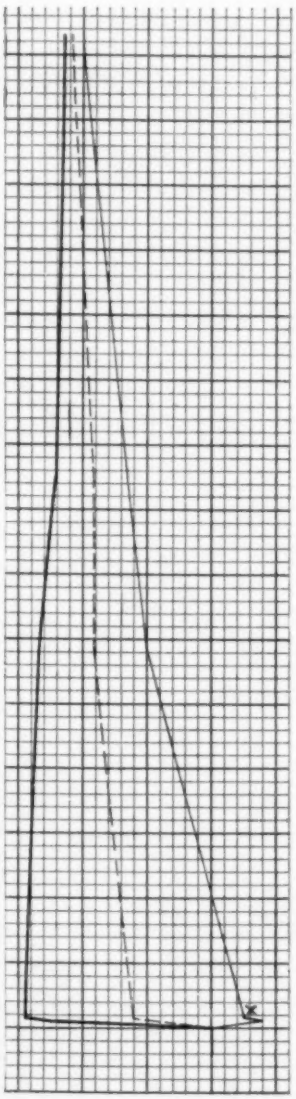

FIG. 8. A graph representing the reaction shown in FIGS. 6 and 7, drawn according to data in TABLE III, on the same scale as FIG. 4.

After a day's rest, the tentacle used in the first experiment was stimulated a second time. The leaf was still fresh and actively secreting. At the beginning of this experiment the tentacle measured 3.37 mm. The results of the reaction are shown in TABLE IV, and are represented in graphical form in FIG. 9. Movement began within two minutes. The bending was produced by elongation of the abaxial side beginning in Segment 6 and extending apically to Segments 5 and 4, and basally to a part of Segment 7. The region of elongation and curvature was shorter than in the first reaction, where it included Segments 3 and 2. The acceleration of the rate of growth was also less than during the first inflexion. The time required for the bending was increased to four hours. The time taken to regain the original position was

approximately the same as before, 22 hours and 45 minutes. At the end of the reaction the tentacle measured 3.74 mm. It had increased 0.37 mm. in length. A control, that like this tentacle

TABLE IV

	No. of Segment	10.15 A. M.	10.30 A. M.	10.45 A. M.	11.00 A. M.	*11.30 A. M.	11.45 A. M.	12.45 A. M.	2.15 P. M.	3.00 P. M.	7.00 P. M.	10.10 P. M.	9.00 A. M.
Abaxial side	1	80	80	80	80	80	80	80	80	80	80	80	80
	2	25	25	25	25	25	25	25	25	25	25	25	25
	3	28	28	28	28	28	28	28	28	28	28	28	28
	4	34	35	35	35	35	36	36	36	36	36	36	36
	5	46	46	49	53	54	55	55	57	57	57	54	53
	6	55	64	64	69	69	69	69	71	71	71	71	70
	7	69	69	69	71	73	76	76	82	82	82	82	82
	Total	337	347	350	361	364	369	369	379	379	379	376	374
Adaxial side	1	78	78	78	78	78	78	78	78	78	78	79	79
	2	24	24	24	24	24	24	24	24	24	24	25	25
	3	27	27	27	27	28	28	28	28	28	28	28	28
	4	34	35	35	35	35	35	35	35	35	35	35	36
	5	46	46	47	47	47	47	47	47	47	47	53	54
	6	55	59	59	59	59	59	59	59	59	59	60	69
	7	75	75	75	75	75	76	77	78	79	84	84	84
	Total	339	344	345	345	346	347	348	349	350	355	364	375

* Controls well bent.

had made one previous inflexion, measured 2.85 mm. before and after the experiment. Another that had never reacted measured similarly 2.3 mm.

This tentacle was allowed to rest over another day and it was stimulated for the third time. At this time it measured 3.74 mm.

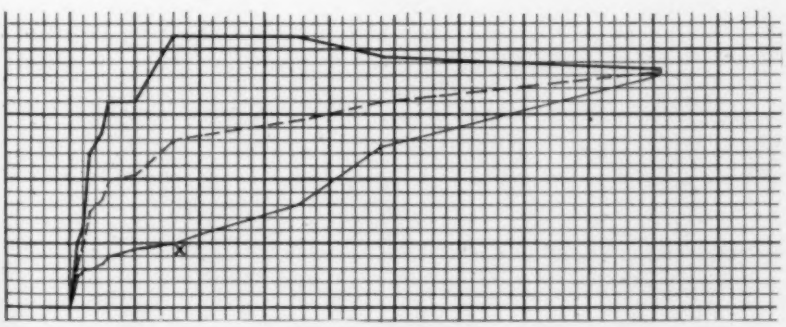

FIG. 9. A graph representing the second reaction of the tentacle shown in FIGS. 1–4; drawn according to data in TABLE IV, and on the same scale as FIG. 4.

The reaction is represented in TABLE V and FIG. 10. No movement was observed for an hour after stimulation. The region of elongation and curvature was shorter than in the second reaction.

TABLE V

	No. of Segment	12.00 M.	2.55 P. M.	7.30 P. M.	10.40 P. M.	9.15 A. M.	1.00 P. M.
Abaxial side	1	80	80	80	80	80	80
	2	89	90	92	92	92	92
	3	53	54	54	54	54	54
	4	70	79	79	79	78	77
	5	82	98	98	98	96	95
	Total	374	401	403	403	400	398
Adaxial side	1	79	79	79	79	79	79
	2	89	94	93	93	93	93
	3	54	53	54	54	54	54
	4	69	68	68	68	75	77
	5	84	84	85	85	90	93
	Total	375	378	379	379	391	396

The acceleration of growth on the convex side was less than in the previous reaction, and the tentacle was not fully bent for 7 hours and 30 minutes. It remained in this condition 2 hours and 30 minutes before unbending again. The tentacle was again straight 25 hours after stimulation. It measured 3.98 mm., an increase of 0.24 mm. After this experiment the tentacle stopped secreting, and no further reaction could be obtained.

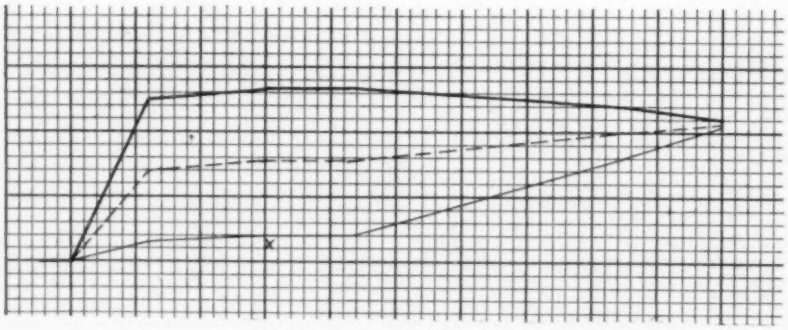

FIG. 10. A graph representing the third reaction of the same tentacle shown in FIG. 9; drawn according to data in TABLE V, and on the same scale as FIG. 4.

The results of the three successive reactions of this tentacle are summarized in TABLE VI. The increase in length for the three reactions was 0.43 mm., 0.37 mm. and 0.24 mm. The region of most intense growth moved basally. In the first reaction

TABLE VI

No. of Segment	Original Length	Length after First Bending	Amt. of Growth	Relative Amt. per Mm.	Length after Second Bending	Amt. of Growth	Relative Amt.	Length after Third Bending	Amt. of Growth	Relative Amt.
1	80	80	0	0	80	0	0	80	0	0
2	47	53	6	13	53	0	0	53	0	0
3	29	34	5	17	36	2	6	39	3	8
4	36	46	10	27	53	7	15	54	1	2
5	43	55	12	28	70	15	27	77	7	10
6	59	69	10	17	82	13	19	95	13	16
Total ...	294	337	43	15	374	37	11	398	24	6

it was in Segments 4 and 5; in the second in Segment 5; and in the third in Segment 6. The ultimate stages of bending in the three reactions are shown in FIG. 11. In each subsequent inflexion

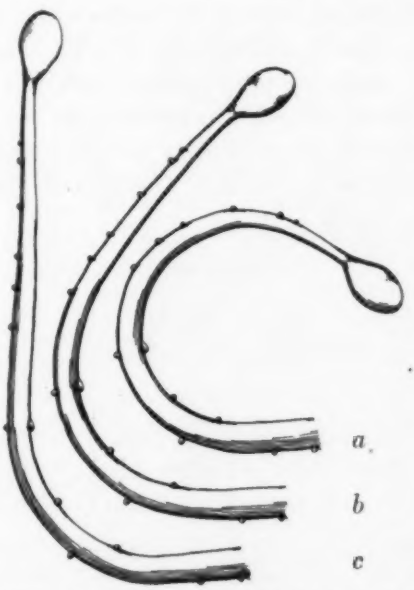

FIG. 11. The ultimate stages in three successive inflexions of the same tentacle, × 22. *a*, at the end of the first inflexion; *b*, at the end of the second inflexion; *c*, at the end of the third inflexion.

the amount of bending decreased, the gland was moved through successively smaller angles and the zone of bending was restricted to shorter and more basal portions of the tentacle.

TABLE VII

No. of Segment	Original Length	Length after First Reaction	Amt. of Growth	Relative Amt. per Mm.	Length after Second Reaction	Amt. of Growth	Relative Amt.	Length after Third Reaction	Amt. of Growth	Relative Amt.
1	23	23	0	0	23	0	0	23	0	0
2	40	40	0	0	40	0	0	40	0	0
3	11	11	0	0	11	0	0	11	0	0
4	22	23	1	5	23	0	0	23	0	0
5	35	34	3	9	41	3	8	41	0	0
6	20	23	3	15	25	2	8	27	2	8
7	21	34	13	62	41	7	21	59	18	44
Total ...	172	192	20	17	204	12	6	224	20	10

TABLE VII shows the growth of another tentacle during three successive reactions. The respective elongations were 0.2 mm., 0.12 mm. and 0.2 mm. During the first reaction Segments 4 to 7 grew. The rate of growth was most intense in the lowest segment and decreased toward the apex. The second reaction was produced by growth in Segments 5 to 7. Segment 4 did not elongate. Here again the most intense growth was at the base. In the third reaction growth was confined to Segments 6 and 7, and was considerably more intense in the latter. Segments 4 and 5 did not increase in length. The tentacle was again stimulated but did not bend.

TABLE VIII

No. of Segment	Original Length	Length After First Reaction	Amt. of Growth	Relative Amt. per Mm.	Length After Second Reaction	Amt. of Growth	Relative Amt.	Length After Third Reaction.	Amt. of Growth	Relative Amt.
1	85	85	0	0	85	0	0	85	0	0
2	52	54	2	4	54	0	0	54	0	0
3	82	88	6	7	89	1	1	89	0	0
4	23	25	2	9	33	8	32	38	5	15
5	36	42	6	17	51	9	21	60	9	18
Total ...	278	294	16	6	312	18	6	326	14	15

A third example of this sort is given in TABLE VIII. The reaction time of the first inflexion was 1 minute, 40 seconds. Segments 2 to 5 increased in length. The rate of growth was

greatest in the lowest segment and decreased apically. The second reaction was produced the day following the first. The reaction time was 1 minute, 30 seconds. Growth occurred in Segments 3 to 5. Segment 2 had stopped growing. The third reaction took place two days after the first one. More than an hour elapsed before movement was detected. Growth was confined to Segments 4 and 5. No elongation of Segments 2 and 3 took place. The third unbending of the tentacle was exceedingly slow, and the pedicel did not regain its original position until three days after stimulation. A fourth reaction could not be induced. The elongations accompanying the first, second and third inflexions were nearly constant, being 0.16 mm., 0.18 mm. and 0.14 mm., respectively.

TABLE IX

No. of Segment	Original Length	Length after First Reaction	Amt. of Growth	Relative Amt.	Length after Second Reaction	Amt. of Growth	Relative Amt.
1	80	80	0	0	80	0	0
2	19	20	1	5	20	0	0
3	20	21	1	5	21	0	0
4	16	18	2	13	18	0	0
5	37	43	6	16	44	1	2
6	32	41	9	28	43	2	5
7	34	44	10	29	49	5	11
Total....	238	267	29	12	275	8	3

TABLE IX gives the growth during two successive reactions of a tentacle. The growing region is much more restricted in the second than in the first bending. In both cases the rate of growth increases toward the base of the pedicel.

(*d*) DISCUSSION

i. *Bending*

The bending of a *Drosera* tentacle is produced by an acceleration of the rate of growth, which extends from the convex side through the middle of the tentacle. In some cases the concave side is likewise included, so that the entire cross-section of the pedicel participates. In other cases the region of accelerated growth stops at a so-called neutral line, somewhere between the middle and the concave side. Under such circumstances the con-

cave side becomes shorter, probably as a result of compression. The acceleration is greatest on the convex surface and diminishes toward the concave. This difference in the rate of growth produces the bending when the acceleration extends all the way through the pedicel and includes the concave surface. If a neutral line is present, it presumably serves as a brace against which the elongation of the convex side acts.

The increase in the rate of growth begins in a part of the pedicel at or near its base, whence it moves toward the gland, widening its scope until one to two thirds of the pedicel is involved. The gland and the adjacent portion of the pedicel do not grow. C. Darwin ('08, p. 9) states that the distal half remains straight in all cases; but growth is not always as confined as he indicates, for in one case (TABLE VIII) 70 per cent of the tentacle grew, and in another (TABLE I) 73 per cent. If the place where the reaction begins is not the most basal portion of the pedicel, the acceleration of the rate of growth extends also a short distance in the direction of the leaf-blade (TABLE I). Those regions where the reaction commences have the highest rate of growth and are involved in the reaction for the greatest length of time: consequently they grow most, so that the amount of elongation is greatest at the base and decreases toward the apex. Ordinarily, bending is confined to one place, but in some of the long marginal tentacles the pedicel curves in two places—in the middle and again at the base (cf. C. Darwin, '08, p. 206). This is particularly characteristic of those tentacles which have the gland imbedded on the upper side of the pedicel, instead of at the apex.

The amount of bending is determined by two factors; the difference between the lengths of the convex and concave sides, and the thickness of the bending region. An increase in the former augments, in the latter diminishes the amount of bending. The longest tentacles bend most, since their growing region has the largest dimensions. The gland may be moved through a wide angle, for example 215 degrees as shown in FIG. 2. C. Darwin ('08, p. 9) describes an instance of movement through an angle of 270 degrees. The time required for bending is very variable. It may be nearly six hours (TABLE II, FIG. 5), or only twenty minutes (TABLE III, FIGS. 6, 7 and 8). C. Darwin ('08, p. 23) once saw inflexion finished in 17 minutes, 30 seconds.

In all cases of direct stimulation of the gland, the bending of *Drosera* tentacles is nastic; the inflected gland always points toward the center of the leaf. The stimulus may be contact, heat, injury or some chemical substance in solution.

When a tentacle reacts to a single stimulation, it begins to unbend immediately after the ultimate degree of inflexion has been reached. This is the case when the gland has been irritated by contact with some object for a limited space of time. If the source of stimulation is not removed, as for example when an insect is caught and digested, the tentacle remains inflected for a period varying from one to eleven days, according to C. Darwin ('08, pp. 11, 195). During the interval between bending and unbending the tentacle does not grow in length.

ii. *Unbending*

The unbending of the tentacle is accompanied by an increase in the rate of growth on the concave side and in the median section. The convex side always contracts so that the so-called neutral line exists somewhere between it and the middle of the tentacle. The acceleration of the rate of growth is characterized by a transverse distribution which is exactly opposite that accompanying bending. Its longitudinal distribution is however identical. The increase in the rate of growth commences opposite that basal portion of the convex side which reacted first, and extends as far apically. Growth is most rapid near the base and becomes less intense toward the gland. The contraction of the convex side is usually restricted to a short basal region.

It frequently happens that the concave grows less than the convex side, since the latter is compressed during the expansion of the tentacle. The concave side may undergo a certain amount of compression during the inflexion of the tentacle, so that the two sides grow and contract approximately equal amounts. The unbending proceeds much more slowly than the bending.

In all probability the unbending of *Drosera* tentacles is autotropic (cf. Fitting, '03, p. 612). The stimulus perceived is the inequality of conditions, pressure, tissue-tension, etc., which is produced on the opposite sides of the originally straight tentacle by its bending. The unbending is therefore of a tropic nature,

since it is a reaction in response to differences existing on the opposite sides of the tentacle. The inflexion and expansion of a *Drosera* tentacle present a remarkable instance of a practically continuous reaction, produced by a single mechanism, but caused by two stimuli of different nature, so that it is partly nastic and partly tropic.

iii. *Growth and Turgidity*

Since the movement of a *Drosera* tentacle is the result of growth, it is always longer at the end of a reaction than at the beginning. The amount of elongation varies from 0.1 mm. to 0.5 mm. This suggests a simple demonstration to show that the reaction is accompanied by growth. If a single tentacle on a leaf is stimulated, it will project a noticeable distance beyond its fellows after regaining its original position. In the field, a *Drosera* leaf frequently has some tentacles longer than other ones in the same row. These inequalities are the result of growth attendant upon reaction, for all the tentacles in one row remain of equal length if not stimulated. Sometimes a small insect is caught by a single exterior tentacle, which carries it to the center of the leaf. The insect is, however, too minute to cause a sufficient impulse to be conducted from the discal to the other marginal tentacles. They do not bend, so that after the reaction is completed they are not as long as the tentacle which was inflected.

Turgidity does not play a part in the movement of the tentacles. This was proved by plasmolyzing bent tentacles in 20 per cent salt solution. The plasmolyzed tentacles remained bent.

A comparison of FIGS. 4, 5 and 8 with graphs of Fitting, which show the haptotropic reactions of tendrils of *Sicyos angulatus* (Fitting, '02, p. 378), of *Passiflora gracilis* (Fitting, '03, p. 577, *fig. 6*) and of *Pilogyne suavis* (*ibid.*, p. 578, *fig. 7*), shows that the mechanics of movement in tendrils and tentacles are the same. Similar figures are shown by Wiedersheim for photonastic reactions of leaves of *Impatiens parviflora* (Wiedersheim, '04, p. 241, *fig. 1;* p. 242, *fig. 2;* p. 244, *fig. 5*), and for thermonastic reactions of the perianth leaves of the tulip (*ibid.*, p. 250, *fig. 8*) and the crocus (*ibid.*, p. 254, *fig. 10;* p. 255, *fig. 12*). It is clear that all these reactions are produced by the same mechanism; rapid growth on the convex side and in the median section with attendant contrac-

tion or a slower rate of growth (*ibid.*, p. 255, *fig. 12*) on the concave side. *Drosera* tentacles are characterized by a contraction of the convex side during expansion; this occurred in one case of a leaf of *Impatiens parviflora* (*ibid.*, p. 242, *fig. 2*).

iv. *Conductivity*

The reaction time represents the interval necessary for the latent period and the conduction of an impulse from the gland to the region where the reaction commences. This region has been shown to be a basal portion of the pedicel, so that the impulse is conducted the entire length of the tentacle. The reaction time usually varies from one to two minutes. C. Darwin ('08, pp. 10, 191) saw movement ten seconds after stimulation. This shows that the rate of conduction can be quite high, for assuming the length of the tentacle (which Darwin does not give) to be 2 mm., the rate of conduction would be 0.2 mm. per second, which is faster than any instance given for the haptotropic reaction of tendrils (Fitting, '04, p. 424). The rate of conduction in tentacles is generally much less (cf. Pfeffer, '06, Vol. III, pp. 93, 94). It should be emphasized that in *Drosera* tentacles stimuli are perceived by cells which are fully grown, and which undergo no further development.

It has not been definitely settled through what tissue impulses are conducted in *Drosera*, but in any case an impulse, in being conducted from the gland to the base of a tentacle, must pass through cells which later react, without producing a response in them. These cells apparently respond only to a secondary impulse released in the basal cells by the impulse conducted directly from the gland. This secondary impulse is conducted in the reverse direction, from the base toward the apex.

v. *Second and Third Reactions*

A tentacle is capable of reacting several times in succession. C. Darwin ('08, pp. 11, 19) observed a leaf inflected three times over insects, and suggested the possibility of more reactions. It is probable, however, that a leaf can clasp insects a greater number of times than any individual tentacle can react, because the capture of such prey does not always necessitate the cooperation

of all the tentacles. Those which remain inactive at one time, might bend on a subsequent occasion. However this may be, no tentacle has been observed to react the fourth time.

The second and third reactions of a tentacle are essentially similar to the first. After two reactions a tentacle is much less sensitive than before, as is shown by the increased reaction time. Each subsequent bending takes longer (cf. C. Darwin, '08, p. 19), but the original position is regained in approximately the same time. The amount of growth does not vary according to any definite rule. It depends rather on external conditions and is apparently uninfluenced by the age of the tentacle. If the external conditions are constant, the amount of growth remains the same. In one example (TABLE VIII) this was approximately the case, the increase in length for the first, second and third reactions being 0.16 mm., 0.18 mm. and 0.14 mm. respectively.

The region of growth is however more restricted in each subsequent reaction, and is confined to more basal portions of the tentacle. TABLE VII shows that 57 per cent of the tentacle grew in length during the first inflexion, 50 per cent during the second, and 32 per cent during the third. In another instance (TABLE VIII) the regions of growth were successively 70, 53, and 27 per cent of the length of the tentacle. In each reaction a certain portion of the tentacle becomes fully grown. A *Drosera* tentacle is therefore characterized by intercalary, basipetal growth. Because of this, the number of inflexions which a tentacle can make must necessarily be limited. It is therefore highly probable that a tentacle would bend a fourth time only under very exceptional circumstances.

Since growth is limited to more basal regions, the thickness of the reacting portion is greater at each successive inflexion. Moreover the greatest difference between the lengths of the opposite sides tends to decrease. Both of these factors cooperate in reducing the amount of bending, so that the gland is moved through successively smaller angles, as shown in Fig. 11.

vi. *Nastic reactions*

In all the experiments described, the glands of the marginal tentacles were stimulated directly, but reactions follow likewise

in response to impulses received by the discal tentacles and conducted to the marginal ones. The mechanism by which these reactions are carried out is identical with that described above.

Numerous experiments were made to determine if the marginal tentacles bent toward the source of stimulation. The discal tentacles on one side of a leaf were stimulated and most of the marginal tentacles which reacted to the conducted impulse, in bending toward the center of the leaf bent likewise in the direction of the source of excitement. In a number of such cases, however, marginal tentacles were observed to bend toward the center of the leaf in a direction different from the point of excitement. One or two instances in which the tentacles bent slightly in the direction of the source of excitement and not toward the center of the leaf seemed to be purely accidental and due rather to irregularities in the contour of the leaf. Nitschke ('60, p. 240) and C. Darwin ('08, p. 198 and *fig. 10*) noticed that when a gland on one side of the disk was stimulated, "the surrounding tentacles" bent to the point of excitement and not to the center of the leaf. The statement by Darwin together with his figure has generally been understood to include the marginal tentacles. He says, however ('08, p. 200): "It is, perhaps, owing to the exterior pedicels being much flattened that they do not bend quite so accurately to the point of excitement as the more central ones." I am convinced that the peripheral tentacles seldom if ever carry out tropic movements.

vii. *Discal Tentacles*

The discal tentacles differ both anatomically and physiologically from the marginal tentacles. The latter are dorsi-ventral and nastic, the former are radial and tropic. The central tentacles do not bend in response to a direct stimulus, but only to a conducted impulse, and always toward the point of excitement. The method used for investigating the mechanics of the movement of the marginal tentacles is not adapted for studying them in the central tentacles. In all probability, however, their movements are likewise the result of differential growth on opposite sides. The angle of curvature is in any case slight. This and the small diameter of the tentacles indicate that the amount of growth is

small. The bending region is confined to a very short basal portion of the pedicel.

Transitions from exterior to central tentacles occur, which exhibit intermediate conditions not only in their structure but also in their behavior. It is probable that some of these tentacles are both nastic and tropic.

8. SUMMARY

1. The red pigment which is found in the leaves and roots of *Drosera rotundifolia* is probably trihydroxymethylnapthoquinone.

2. The rosette habit is conditioned by transpiration.

3. The inflexion of *Drosera* tentacles is produced by an acceleration of the rate of growth on the convex side and in the median section. The unbending is caused by an increase in the rate of growth on the concave side and in the median section, accompanied by compression of the convex side.

4. In both cases the acceleration commences near the base and extends toward the gland. The amount of growth is greatest near the base and decreases apically.

5. A tentacle is capable of reacting three times. During each reaction an apical portion of the bending region becomes fully grown. *Drosera* tentacles have intercalary, basipetal growth.

6. The bending of the exterior tentacles is nastic; of the central tentacles, tropic. The unbending is in all cases owing to autotropism.

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The thermometric movements of tree branches at freezing temperatures*

C. C. Trowbridge

(WITH NINETEEN TEXT FIGURES)

During the winter of 1910, the writer of the present paper noticed that the branches of several linden trees on the grounds of Columbia University in the City of New York changed their position when a fall of temperature below freezing occurred.

FIG. 1. Photograph showing the extent of the change of the position of a branch of a European linden tree (*Tilia europæa*) between normal and about twenty-two degrees below freezing, Fahrenheit. The lower branch (*M*) has been artificially inserted in the photograph to show extent of movement. Lower branch, at elbow, *M*, 5.33 ft. elevation, temp. + 10° F., February 10, 1912. Upper branch, at elbow, *N*, 6.82 ft. elevation, temp. + 35.6° F., February 28, 1912. This branch is designated as "Branch *A*, Tree No. 1," in the accompanying curves.

[1] Contributions of the Phoenix Physical Laboratory, No. 34.

The matter was again strikingly called to mind during an exceedingly cold period in the early part of February, 1912. As the phenomenon seemed not to be generally known among botanists, a series of measurements was made to ascertain the extent of the movements, and, if possible, to learn something of their origin.

During the course of the work, two or three papers on the subject came to light, two of which anticipated the observations of the writer with respect to the general phenomena of the thermometric movements of branches of large trees. Since, however, the field of the investigation has been extended in several respects, and because the matter is so little understood, the observations made are published in full in the present paper.

The general facts relating to thermometric movements of branches of large trees as based on the writer's observations are as follows: It appears in the case of certain species, particularly the European linden (*Tilia europaea*), that when the temperature of the air reaches the freezing point of water, 32° F. (0° C.), the branches of the tree, large and small, begin to bend and continue this movement with further reduction of temperature. At the lowest temperature measured, about 0° F. (− 17.5° C.), the ends of the large branches of a particular linden under observation showed depressions as great as from three to five feet below their position at 32° F. The movements of the branches were found in general to correspond closely to the changes in temperature of the surrounding air, as will be shown. The observations made consisted of daily and hourly records of the height of branches of several species of trees with corresponding meteorological data. The work has been supplemented by photographs. The relation of the air temperature and the relative humidity to the observed changes in the branches will be presented in the form of curves.

The subject is an important as well as an interesting one, since frost cracks of the linden have been found by the writer to accompany in no accidental manner the thermometric movements of the branches. Frost cracks have much to do with the injury to various trees by insects and by decay, a matter well known, and at present a subject of investigation by the Bureau of Plant Industry of the Department of Agriculture of the United States.

Historical

A brief summary of the contents of papers relating to the subject of this paper is given below.

It is a noteworthy fact that comparatively little is to be found in the literature on the thermometric movement of branches of trees. Moreover, references in recent botanical papers to the few contributions on the subject are rare indeed; it is for this reason that the phenomenon is not well known among botanists. The writer was at first unable to find any published account of the gross thermometric movements to be described, but after the observations had been partly completed, his attention was called by Dr. J. T. Grossenbacher, of the Bureau of Plant Industry, Washington, D. C., to two papers on the subject, one by Robert Caspary, and the other by N. Geleznow, which were published in 1866 and 1872 respectively. Dr. Grossenbacher, having observed an abstract of the writer's observations,* published an article chiefly devoted to a discussion of these two early researches.† To quote from a footnote in his paper: "This review of the literature of branch movements and observations grew out of a study of crown-rot of fruit trees and is published separately because it is only indirectly related to the main theme." Owing to the publication of a review of these papers, they are referred to more briefly in the present paper than otherwise would have been the case.

Mr. John Rogers, at Kent, England, was apparently the first to observe the movement of large branches of trees in cold weather. His first observations were made as early as 1838, and a short note on the observations was published a few years later.‡

In 1865, Professor Caspary, of Königsberg, made a series of measurements of the phenomenon observed by Rogers, on a number of species of trees in the Königsberg botanical gardens. The observations were published under the title, "Über die veränderungen der Richtung der Äste holziger Gewächse bewirkt durch niedrige Wärmegrade."§ Caspary found three types of

* Branch movements of certain trees in freezing temperatures. Torreya 13: 86–87. 1913.

† Branch movements induced by changes of temperature. Science II. 38: 201–205. 1913.

‡ Trans. Hort. Soc. London II. 2: 230. 1842.

§ Internat. Hort. Exhib. Bot. Congress 98–117. 1866.

FIG. 2. Photograph of European linden tree No. 1, when the air temperature was + 50° F. Branches at normal level. Note positions of branches at *A*, *B*, *C*, *D* and *E*.

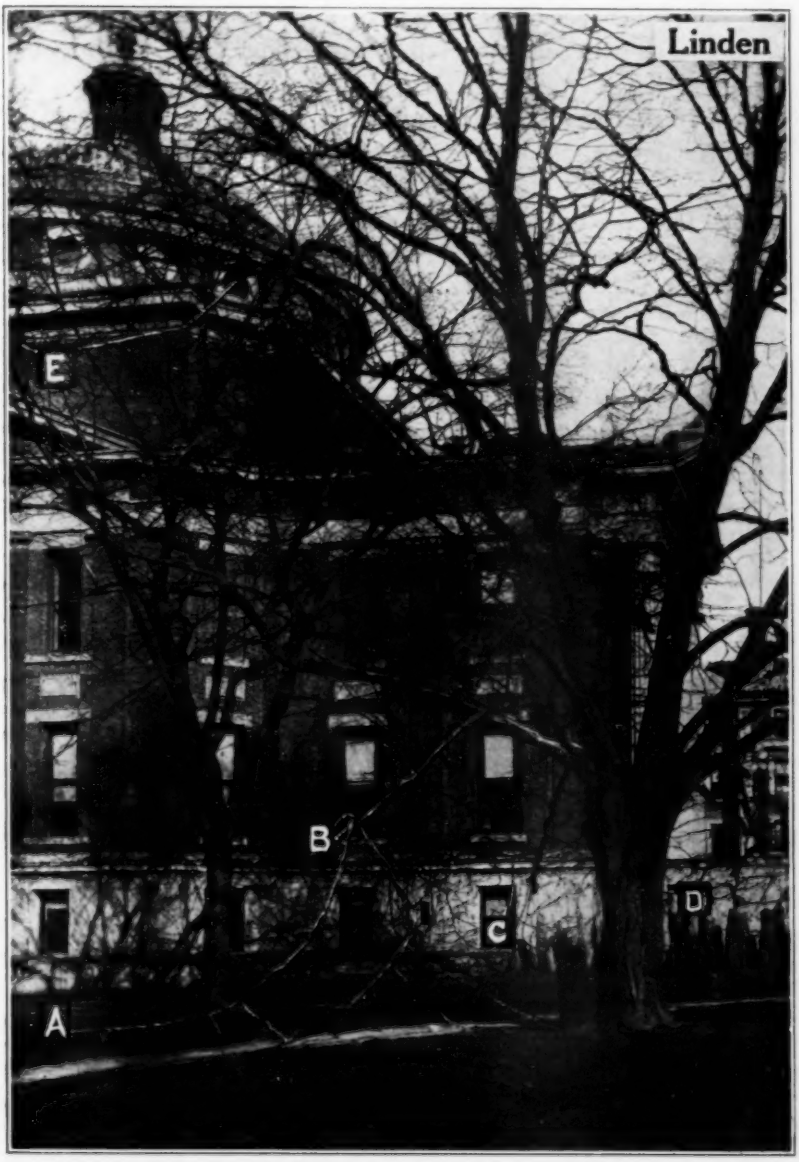

FIG. 3. Photograph of European linden tree No. 1 at + 14° F. (18° below freezing) showing marked depression of branches. See position of branches at *A*, *B*, *C*, *D* and *E*.

movements accompanying a fall of temperature. In one class, (*a*), the branches became depressed; in the second, (*b*), they rose at first, then with continued fall of temperature became depressed; and (*c*) they became elevated without being depressed. The measurements were carefully made on ten species of trees. No definite conclusion, however, as to the cause of the movements was arrived at by Professor Caspary, although he suggested the theory that the movements were caused by a differential expansion between the upper and lower sides of the branches.

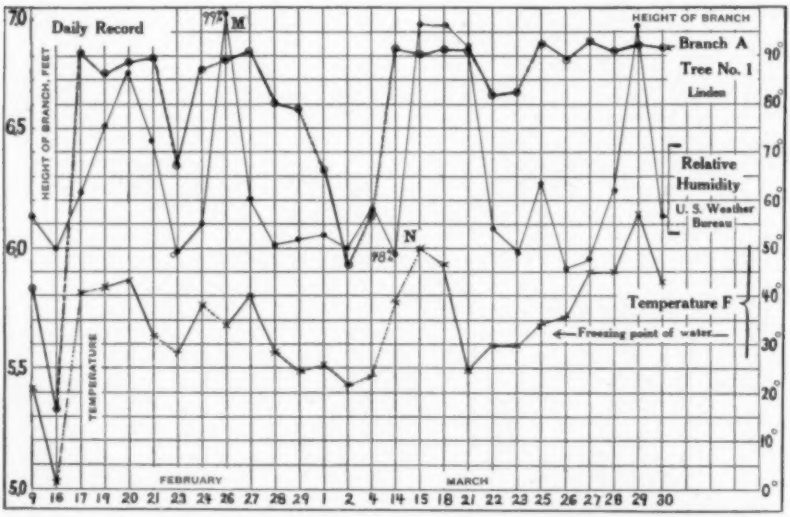

FIG. 4. Daily record of Branch *A*, Tree No. 1 (European linden) during *February* and *March*, 1912. Broken lines indicate where the daily record was not continuous. The branch movements are seen to follow closely the air temperature changes when *below freezing*. The amount of atmospheric moisture present, as shown by the relative humidity record (fine line curve), apparently has little effect on the position of the branch.

Later the following paper appeared: "Recherches sur la quantité et la répartition de l'eau dans la tige des plantes ligneuses," by N. Geleznow.* This contribution deals chiefly with the amount of moisture in the various parts of branches and tree trunks. Observations on the change in the position of branches with change of temperature were also made. Geleznow stated that he had first noted the phenomenon in 1854–5, and experiments made by him in 1864 and 1865 showed that the excentric

* Bull. Acad. Imp. Sci. St. Petersburg **9**: 667–685. 1873–1877.

position of the medullary canal in some species had a marked influence on the phenomenon, but there were some anomalies which could not be explained. Experiments made in 1865–1867 showed a slight relation of the water content of the branches to the thermometric movement of the branches, but the connection was not at all definite. The work was undertaken largely to find an explanation of Caspary's work at Königsberg, already referred to.

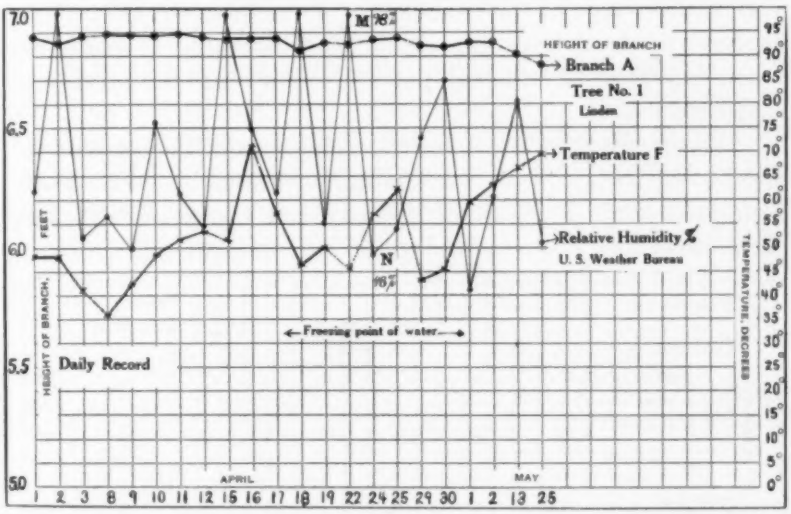

FIG. 5. Daily record of Branch 'A, Tree No. 1 (European linden) during *April* and *May*, 1912. Little or no movement appears to accompany the large changes of both the air temperatures (all above 32° F.) and the relative humidity. The depression in the branch during *May* is due to the weight of the leaves.

A letter in Nature, entitled, "Position of boughs in summer and winter," by Agnes Fry,* records the height of branches of both a mulberry and a walnut tree in summer and in winter. The measurements show the reduced height in summer due to the weight of the leaves. The changes amounted to one foot or slightly more. This note is not pertinent to the subject under discussion since the movements observed were not thermometric.

In 1898, there appeared a paper of similar character to the last, entitled, "Preliminary observations of the seasonal variation of a branch of a horse chestnut tree," by Miller Christy.†

* Nature 54: 198. 1896.

† Jour. Linn. Soc. Bot. 33: 501. 1898.

The measurement reported consisted in the change in height of a branch of this species due to the growth and to the fall of the leaves. The height decreased in April and May, coincident with the growth of the leaves. Then followed a period of rest, but in August and September there was a further depression. In October, the branch rose with the fall of the leaves, the maximum variation being about one foot. "During the winter months, very little change in the elevation of the branch was observable, as shown by the observations, etc." No temperature changes were recorded. It is seen that this paper does not relate to the problem under discussion.

"An undescribed thermometric movement of the branches of shrubs and trees," by W. F. Ganong,* is in some respects closely connected with the work of Caspary and Geleznow and with the observations made by the writer of the present paper.

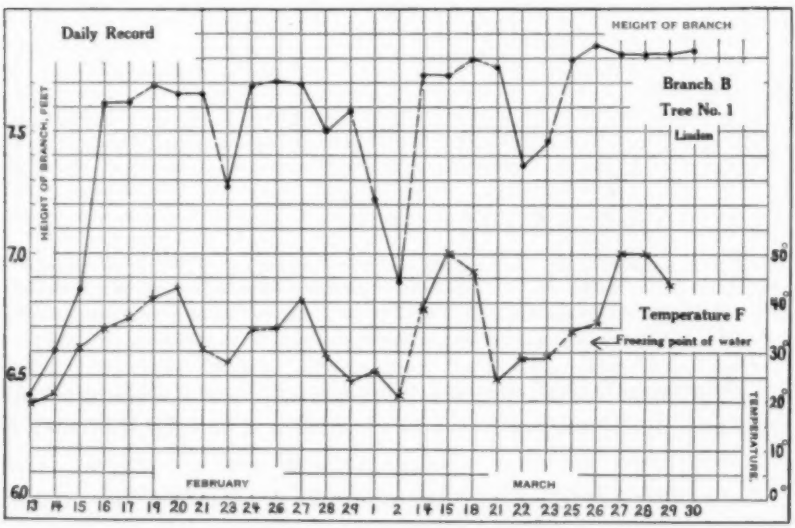

FIG. 6. Daily record of the movements of Branch *B*, Tree No. 1 (European linden) during *February* and *March*, 1912. The movements correspond closely with those of Branch *A*, in FIG. 4, although some of the observations were on different days.

Ganong's observations related mostly to the movements of twigs of shrubs and very small trees, and scarcely exceeded 12 cm. There is no mention, moreover, of the important fact (as

* Ann. Bot. **18**: 631–644. *f.* 52–57. 1904.

in the case of large trees) that the movement begins when the temperature of the air reaches the freezing point of water.

Two movements are described, a gradual seasonal displacement, and a secondary, depending indirectly on thermometric changes. Whether the latter is similar to the one to be described is difficult to ascertain. Ganong has performed some important experiments, and concludes that the secondary movements are correlated with changes in temperature *but that they are not directly caused by temperature.*

Miss Jean Broadhurst * is the author of a note entitled, "The weeping willow in winter," describing the observation that the slender unbranched twigs of this tree (twigs one to two feet long), which in November hang vertically, become curled up during the early winter so that the ends of the twigs are above their origin. The phenomenon appears to be a seasonal one rather

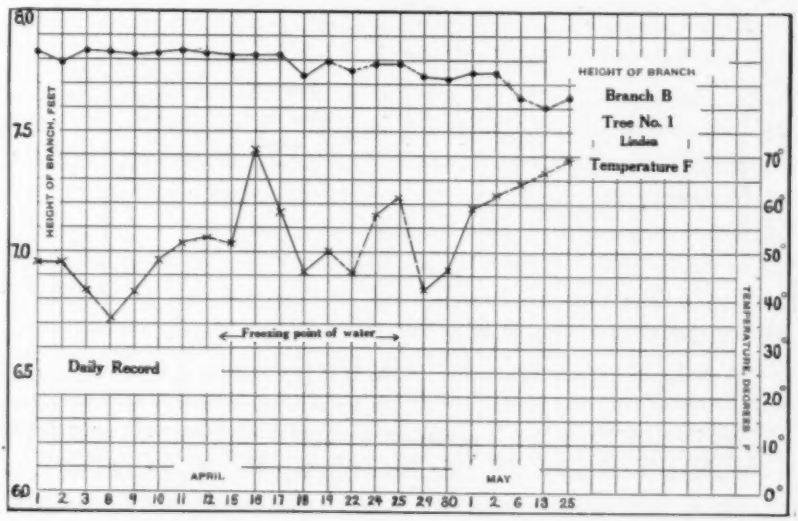

FIG. 7. Daily record of Branch *B*, Tree No. 1 (European linden) in *April* and *May*, in 1912, showing the same effect exhibited by Branch *A*, in FIG. 5, including the drooping in May due to the weight of the leaves.

than one depending on temporary temperature conditions. A further note on the subject entitled, "Winter changes in the weeping willow," was published later.† It is possible that the

* Torreya **10**: 38, 39. 1910.

† Torreya **14**: 31, 32. 1914.

movements here described may be similar to those made on small shrubs by Ganong.

OBSERVATIONS BY THE WRITER IN 1912 AND 1913

The measurements conducted during the early part of 1912, described below, were not made under the most favorable circumstances, because it was near the end of the winter when the striking effects were noted and the measurements begun; also, there were few unusually cold periods during the winter of 1912–13. Enough observations, however, were taken to exhibit some interesting facts. Most of the observations in February, March, April and May, were made with Mr. E. Sweitzer, a special student in Columbia University. The observations during the winters of

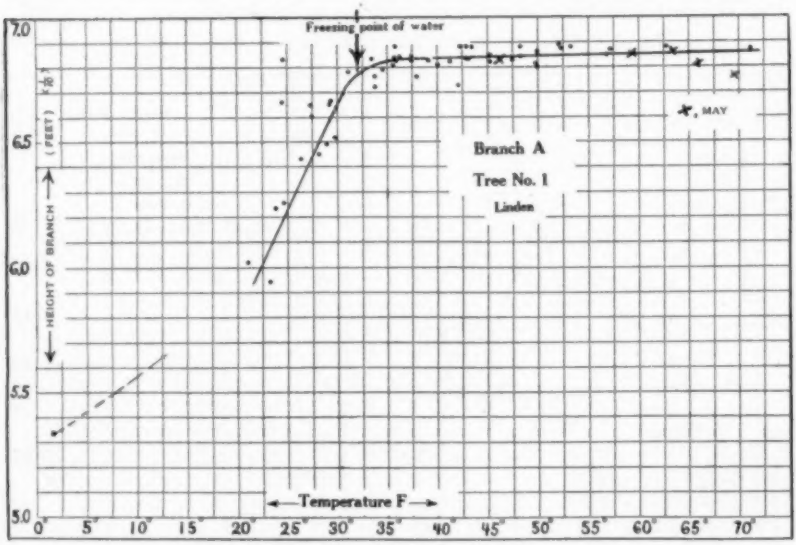

FIG. 8. Curve showing the relation of temperature change to height of branch in the case of Branch *A*, Tree No. 1 (European linden). The curve shows a point of inflection at the freezing point of water. The variation among the observations is due to temperature lag or to strain in the branch as determined by hourly records of the thermometric movements.

1913–14 and 1914–15 were more extended and were made by the writer alone.

A study of movements of the branches of trees under freezing temperature was taken up solely on the physical side of the sub-

ject, the problem being to find the atmospheric conditions under which the movements took place, and to determine the extent of the effect produced. To illustrate the interesting phenomenon under discussion, photographs (FIGS. 1–3) have been taken.

In FIG. 1, the extent of movements can be seen at a glance. The photograph has been artificially arranged with the addition of a duplicate photograph of a branch, fitted in according to scale, and is given here solely to show the magnitude of the effect. The upper branch shows the position as it was at 32° F. or above; and the lower one, the same branch as it was at approximately 10° F. This very large movement shown indicates some interesting processes going on within the living portion of the branch.

METHOD OF MEASUREMENT AND SPECIES OF TREES STUDIED

The apparatus used consisted of a specially constructed measuring rod, a steel tape, and thermometers. The linear measurements are given in feet and hundredths of feet. The temperatures are given in Fahrenheit as being more convenient, although many sets were taken in Centigrade. The Fahrenheit scale was used to compare temperatures with temperatures taken from a record of the United States Weather Bureau, which are expressed in Fahrenheit. Also, the temperature curve continually crossed the freezing point of water; hence the use of the Fahrenheit scale avoided the employment of the + and − sign. The heights of four branches from the ground were measured, three species of trees being selected, and also the distance from the point on the branch measured, as indicated by a plumb line, to the trunk of the tree in a horizontal line. The latter measurements are not given in this paper, since they correspond in general to the vertical measurements.

Two similar curved branches of a European linden tree designated as Tree No. 1, were measured; also, a branch of a *Paulownia tomentosa*, designated as Tree No. 2, similar in shape to the branches of Tree No. 1, and a horizontal branch of an oriental plane-tree or sycamore (*Platanus orientalis*) recorded as Tree No. 3.

It was to be regretted that branches of the linden of various shapes were not measured, but the observations that were made

absorbed a good deal of time, and the desirability of an extension of the records to branches of different forms was not foreseen.

Temperature and relative humidity observations taken from the United States Weather Bureau have been used in a few cases. The Draper Observatory in Central Park, where these observations were made, is not more than three miles distant from the Columbia University grounds, and since it was shown by the thermometer records at the two places that the temperatures were usually within a degree or so of each other they agree sufficiently in the present case. No relative humidity observations were made, but the Draper Observatory record of the moisture was sufficiently

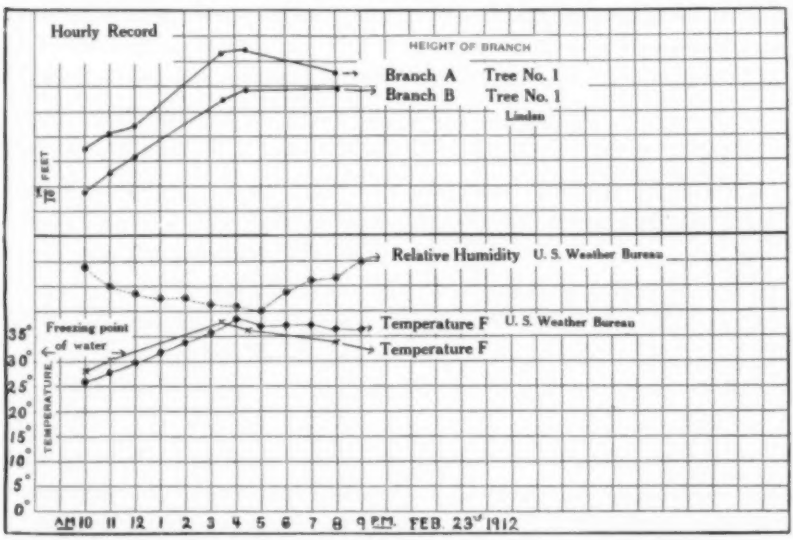

FIG. 9. Hourly record of Branches *A* and *B*, Tree No. 1 (European linden), showing rise of temperature through the freezing point and subsequent fall. Here the branches appear to respond quickly to the changes in temperature and there also appears to be a slight thermometric movement *above freezing*.

close for the use to which it was put, since large changes in relative humidity appeared to have little or no effect on the position of the branches.

DAILY RECORDS AND EXPLANATION OF CURVES SHOWN IN FIGS. 4, 5, 6, 7 AND 8

The daily record of Branch *A*, Tree No. 1 (linden), is given in FIGS. 4 and 5, for February, March, April and May. The facts shown by these curves are as follows:

The temperature when above 32° has little effect on the position of the branch, but whenever the temperature of the air passes below the freezing point of water, an immediate bending of the branches of the tree takes place. Throughout April and for some observations in May, very little change in the position of the branch takes place, except depression of the branch due to the weight of the leaves in May. Notwithstanding the fact that during April and May there was a large variation in temperature, no movement took place because all the temperatures were above 32° Fahrenheit. In regard to the influence of water vapor present in the atmosphere on the movement of the branches, it can be seen by the fine line curve in FIGS. 4 and 5, representing relative humidity, that there is little, if any, effect. This is specially evident at points *M* and *N* in both figures, where the humidity was high and low respectively with apparently little influence on the height of the branch. The curves in FIGS. 6 and 7

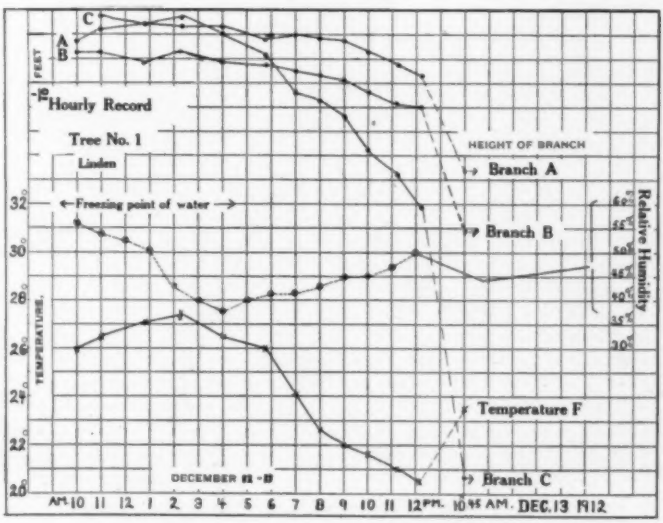

FIG. 10. Hourly record of Branches *A*, *B*, and *C*, Tree No. 1 (European linden). Temperature on a large scale. Branch *C* observations were made at the extremity of a branch. The last reading was taken at 10.45 a.m., the previous observation at 12 midnight preceding.

made with a different branch show effects similar to those observed in the case of Branch *A*. The curves corresponded very closely

for Branches *A* and *B*, except that the days of observation were somewhat different. In FIG. 8, the relation of the variation in height of Branch *A* (same as FIGS. 4 and 5) to the variation of temperature is shown. It is seen at once that there is a marked point of inflection of the curve at the freezing point of water. The fact that the observation points do not fall on the curve is significant and will be presently explained. While the major effect of the temperature is below 32° F., there is evidently a minor thermometric effect just above 32°, which, however, is so small as perhaps to be due to a warping of the branch due to internal strains arising from the bending of the branch, caused by below freezing temperatures a short time before the observations at warmer temperatures were made. Thus the behavior of the branch depends somewhat on its immediately previous history.

HOURLY RECORDS AND EXPLANATION OF CURVES IN FIGS. 9, 10 AND 11

In these curves, an hourly record was kept of several of the branches of Tree No. 1 to ascertain how soon the branch responded

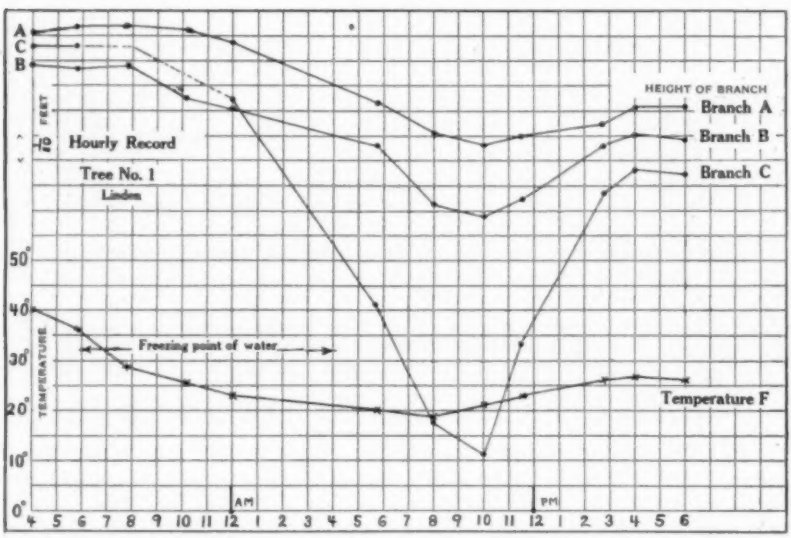

FIG. 11. Hourly record of Branches *A*, *B*, and *C*, Tree No. 1 (European linden), showing the effect of a fall in temperature below freezing and the subsequent rise. Observations of Branch *C* were at the end of the branch. These curves demonstrated the lag in the movements of the branches with fairly rapid changes of temperature and explain the variations among the observations shown in the curve in FIG. 1.

to the changes in the temperature of the air. While observations were not taken every hour, they were frequent enough to obtain the results required. It is seen in FIG. 9, which gives observation where the temperature rises to a maximum just *above the freezing point of water*, that both branches begin to fall with the temperature within a quarter of an hour after the high point of the temperature has been reached and before the temperature passes through the freezing point. This seems to show that there is a very small thermometric effect just above 32° F. The same fact is indicated in other observations. In FIG. 10, three branches were measured and the resulting curves show the effect on the

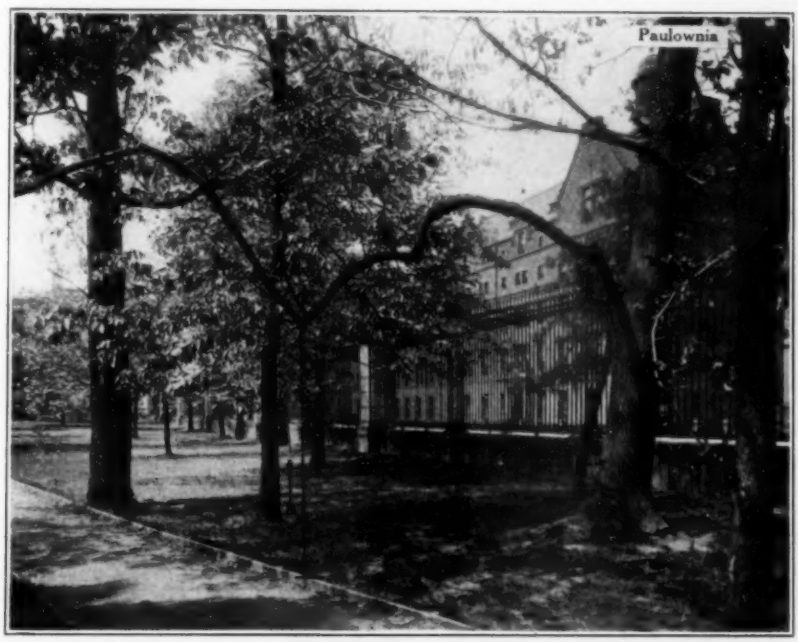

FIG. 12. Photograph of Branch *A*, Tree No. 2 (*Paulowina tomentosa*). This branch showed little or no thermometric changes. The branch was selected because of its similarity in shape to Branches *A* and *B*, Tree No. 1.

branches when the temperature of the air *rises to a maximum, below the freezing point of water*, and then falls again. C observations in this set were taken at the extremity of the branch and hence show the largest movement.

In FIG. 11 the readings of three branches were taken under conditions where the temperature had fallen to about 20° F. and then rose. Here it is clearly shown that there is a lag amounting in time to about two hours before the branches begin to move upward, although a change in the *rate of the depression* is observed to take place as soon as the temperature of the air begins to rise. The effect on the branch of a change of temperature is therefore almost immediate with a lag depending on various conditions. It is probable that the size of the branch is the ruling factor, the very small branches responding almost at once to change in temperature.

EXPLANATION OF CURVES SHOWN IN FIGS. 13 AND 15

In FIG. 13 the daily record from February to May of a *Paulownia* (*P. tomentosa*), Tree No. 2, is shown. The branch measured has the same shape as that of the linden branch shown

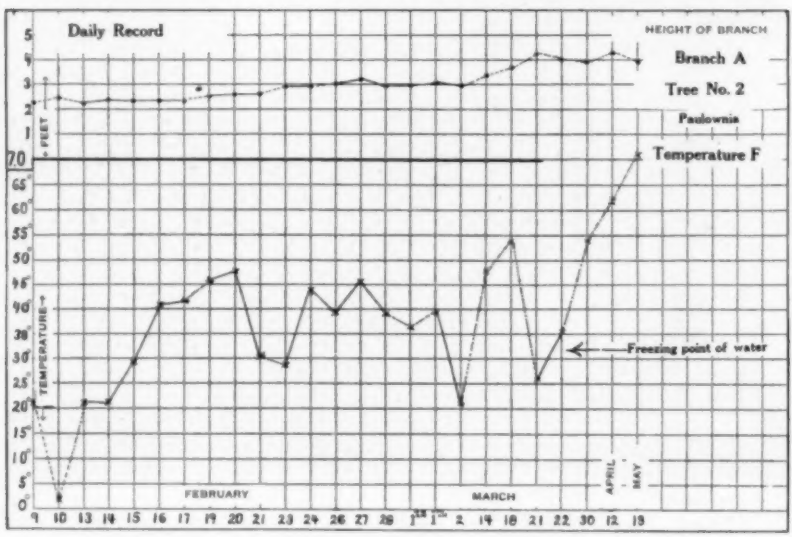

FIG. 13. Daily record of Branch *A*, Tree No. 2 (*Paulownia tomentosa*). Record for *February*, *March*, *April* and *May*. No appreciable change is shown which accompanies below freezing temperatures,—but a gradual rise from February to May is evident and a particular response to warm days during that period is apparent.

in FIG. 1. Here it is seen that there is little or no thermometric effect due to the changes of temperature of the air, although the

temperature repeatedly passed through the freezing point of water. There is, however, a continual rise of the branch from ear y in February till May. This elevation is evidently a response to heat and light of the sun, and being a seasonal change, is an entirely different effect from that observed in the linden.

FIG. 14. Photographs of Branch *A*, Tree No. 3, sycamore (*Platanus orientalis*). Measurements shown in FIG. 15. This branch differed from others measured in being straight and nearly horizontal.

In FIG. 15 an intermittent record of the height of a straight branch of a sycamore tree, *Platanus orientalis*, Tree No. 3, from February to well along in April, is given. Here also no thermometric movement is observed, the gradual rise of the branch recorded being a seasonal change. These observations merely show that in certain trees there is no thermometric movement of the branches.

THE ELASTIC CONSTANT OF BRANCHES ABOVE AND BELOW FREEZING

In FIG. 16 s shown a plot of an experiment which consisted in weighting the branches of both Tree No. 1, the linden, and Tree

No. 2, the *Paulownia*. Sixty-five pounds were added to the branch, five pounds at a time. This experiment was made both at a temperature above freezing, and also at a temperature well below freezing. It is seen that the constant of elasticity has changed in both cases, and the amount of depression per pound has decreased for the branches of both trees at the lower tempera-

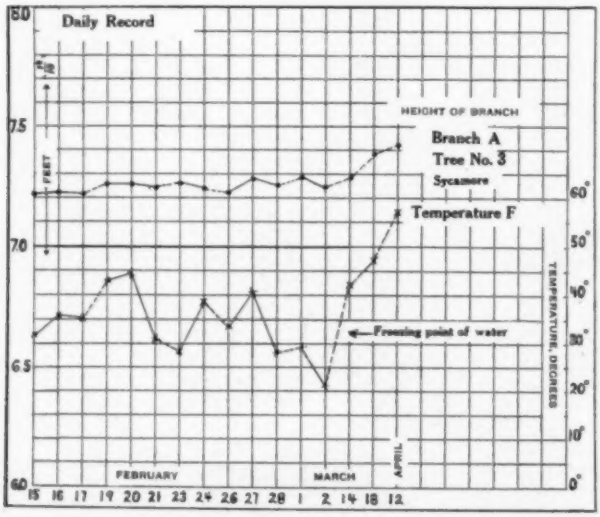

FIG. 15. Daily record of height of Branch *A*, Tree No. 3 (sycamore), during *February*, *March* and *April*, showing no effects due to variation in air temperatures, below freezing, but a rise beginning in February, with a more decided increase in elevation in March and April, especially accentuated on warm days.

ture. It would therefore appear as if the change in the modulus of elasticity of the two branches, due to changes in the temperature, had little or nothing to do with the direct temperature effect produced in the case of Tree No. 1, the linden, which showed large thermometric movements.

From theory it is to be expected that if there is a change in the modulus of elasticity due to temperature, and if a stiffening occurs at low temperature, the branch would not be as much depressed. Such an effect is opposite to the large thermometric movement actually observed. In the case of the weighted cold branches a loss in recovery is noted, which is probably temporary, but explains certain inconsistencies observed on other observations.

The following experiment was tried. A branch, curved in form, was cut from the linden and at once artificially cooled to 0° F., in a salt-ice pack, but showed no change of curvature between 0° F. and 40° F. The experiment, however, was not conclusive, since the branch was not longer than about three

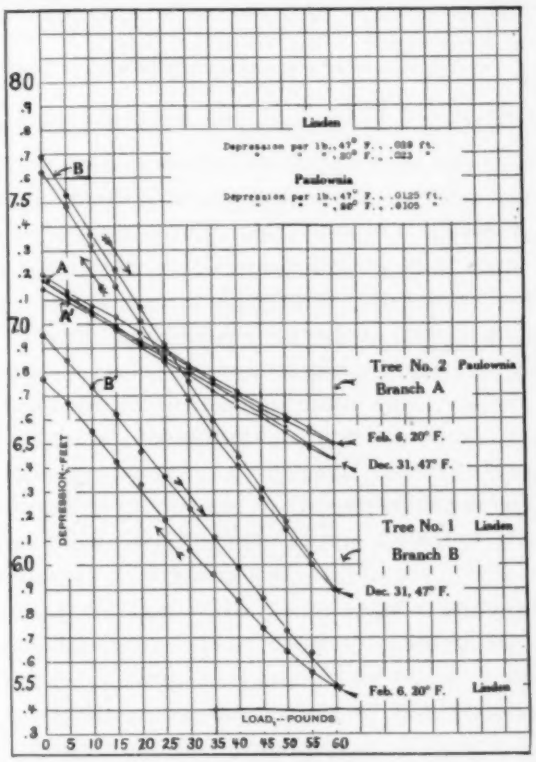
Linden
Depression per lb., 47° F. . .009 ft.
" " " 20° F. . .023 "
Paulownia
Depression per lb., 47° F. . .0125 ft.
" " " 20° F. . .0105 "
B
A
A'
B'
Tree No. 2 Paulownia
Branch A
Feb. 6, 20° F.
Dec. 31, 47° F.
Tree No. 1 Linden
Branch B
Dec. 31, 47° F.
Feb. 6, 20° F. Linden
DEPRESSION, FEET
LOAD,-- POUNDS
0 5 10 15 20 25 30 35 40 45 50 55 60

FIG. 16. Effect of loading Branch *B*, Tree No. 1 (European linden), and Branch *A*, Tree No. 2 (*Paulownia tomentosa*), at two differentt emperatures. The modulus of elasticity constant is less in both cases at temperatures below freezing, which is to be expected. A change of the constant, therefore, does not account for any part of the depression of the branches *A*, *B* and *C*, Tree No. 1 (linden), with low temperature since the effect of the change of the modulus is opposite to the thermometric movement observed.

feet. It was ascertained definitely, however, that certain branches which were curved upward on the linden became more curved when subjected to low temperature. This fact was found by attaching strings to the ends of branches which were curved

concave upward, and observing the change of the tension on the reduction of temperature. These cords which were taut at 32° F. (or 0° C.), sagged at 15° F., showing an upward movement of branches which were concave upward. This is in agreement with observations made by Geleznow, who cut off branches, inverted them, and observed that their movement was opposite to those in the normal position.

RELATION OF FROST CRACKS TO THE THERMOMETRIC MOVEMENT

It was noticed both during the winters of 1911–2 and 1912–3 that a linden showed a decided so-called frost crack or longitudinal cleft which was wide open during cold snaps, and in one case, the crack was extended for fifteen feet along the trunk. The width of this crack varied with the temperature and closed up completely as soon as the temperature rose to 32° F. This was particularly noticeable during the coldest period of about February 10, 1912. Frost cracks in the linden are evidently due to the same origin as, or connected with, the thermometric movement of the branches, and therefore their study is intimately associated with the main theme of this paper.

The fact that frost cracks open in cold, and close in warm weather is well known.* In this connection an interesting and reliable observation reported to the writer illustrating the well-known noises caused by frost cracks is as follows. In very cold weather some lindens in a certain grove produced such loud and sharp noises that they were thought to be pistol shots, but were found to be the sudden formation of cracks in the lindens which were observed at the time.

In FIG. 17 a frost crack in a linden is shown, which was about three-quarters of an inch broad. Measurements of this crack with curves of the tree temperatures are given in FIGS. 18 and 19.

The facts shown by these curves indicate that the frost crack is not caused by a difference of temperature at successive depths of the tree trunk, but is due rather to a thermometric effect of some sort, not necessarily ordinary thermal expansion, acting on the cells of the tree, and probably those just below the bark.

* See J. G. Grossenbacher, Science II. 38: 204. 1913.

In FIG. 18 the frost crack is shown closing rapidly when the "Bark" (one inch deep) and the "Medium" (three inches deep) rise abruptly, while the "Deep" thermometer (five inches deep) remained nearly constant. In FIG. 19 the Deep thermometer is still below 19° F. while the frost crack is nearly closed. Moreover, in both sets of observations, the frost crack appears to close with the rise of temperature of the surface layers of the trunk.

THE ORIGIN OF THE THERMOMETRIC MOVEMENT

While there may not yet be sufficient data on which to formulate a theory for the actual mechanism of the thermometric bending of the branches, there are some salient facts which indicate the origin of the phenomenon. It has been shown, at least so far as the linden is concerned, that the movement begins when the air temperature is at the freezing point of water. The internal temperature of the small branches could not be far from that degree of cold.

In the curves published by Caspary* on the European linden showing the branch movements with temperature, there is correspondence between the temperature and branch positions, which indicates that the depressions of the branches began at the freezing point of water, but there is no mention of this in his text. Owing to the fact that a number of trees were studied, which showed various behavior with change of temperature, the matter might well have been overlooked. This opinion seems to be substantiated by the following quotation from Caspary's paper:

"Der Grad der Kälte, bei welcher ein Sinken eintritt, kann wegen Mangel stündlichen Beobachtungen und Beobachtungen der Kälte des Holzes selbst im Innern nicht sicher angegeben werden."

Besides the linden, measurements of trees of various other species by Caspary show that the movement begins at approximately 32° F. By making hourly observation, not made hitherto, the writer has brought out some important facts; namely, that below freezing the branches respond to the changes in temperature almost immediately. Thus, as shown by the curves in FIG. 11, when the temperature falls to 20° F., and then rises, the branches at once slow up in their downward movement, and shortly after-

* Loc. cit.

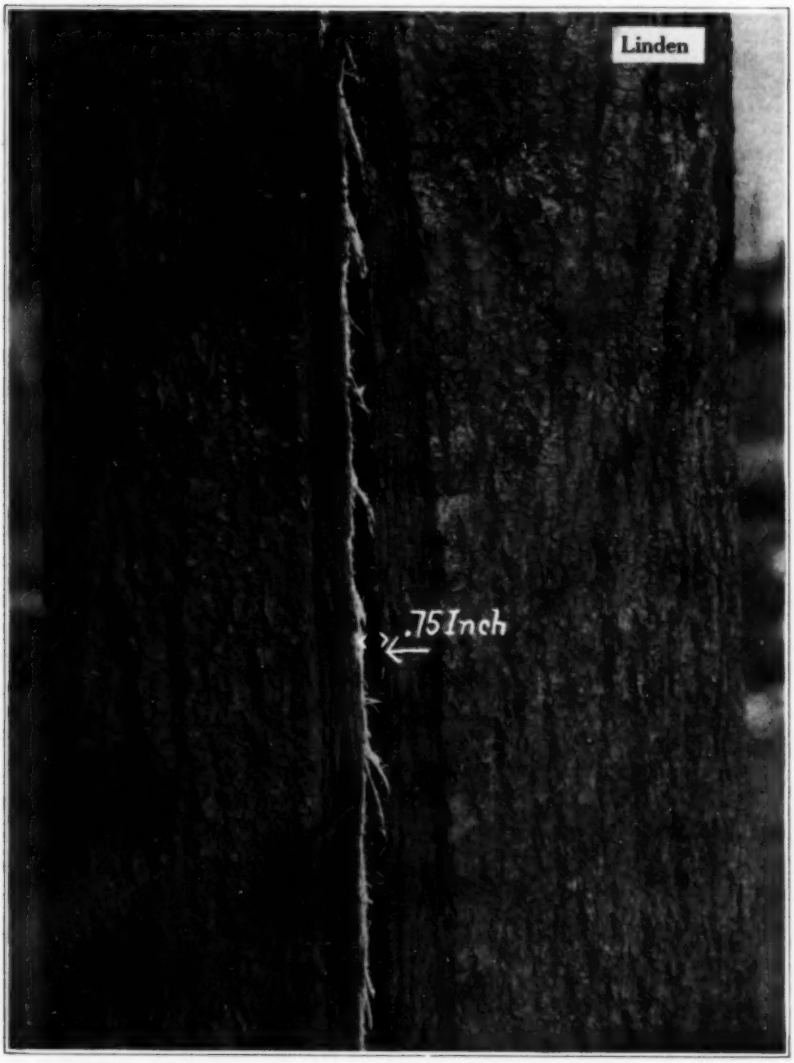

FIG. 17. Frost crack in European linden which opened and shut with changes of temperature and corresponded with movements of the branches. The measurements shown in FIGS. 18 and 19 were made on this tree.

wards move upwards. If the water in the branches was freezing as pure water, then the branches would continue to descend while the temperature remained below freezing, since ice would continue to form at any temperature below freezing. On the other hand, sap from the standpoint of physics is a solution, composed of salts of metals and of dissolved organic substances, and, as such, must freeze fractionally as the temperature is reduced. The sap thus becomes more concentrated as the freezing process continues. On a rise of temperature a fractional melting occurs.

In general, in the case of a solution composed of some salt, a point is reached where the solution will freeze at a definite temperature (in a manner similar to pure water); namely, when the solution reaches a certain degree of concentration. The indications are thus that it is the sap content of the branch rather than the water content which plays the important rôle in the thermometric movements of branches. Geleznow studied the water content of branches with little success in so far as determining the cause of the thermometric movement, and in the light of the explanation given above, negative results should be expected from a study of the water content. The mechanism bringing about the branch movements may well be a process in the living cells where enormous tension is produced in some way from the gradual separation of the ice crystals from the sap, the latter concentrating as the fractional freezing process advances. If this partial explanation is the true one, it should be expected that at some low degree of cold, certain trees would cease to show a thermometric movement of the branches, the sap having reached the so-called cryohydrate concentration where the solution would become solidified. Since the sap is a complex solution, the temperature of complete solidification would probably not be a definite one.

The question of the freezing of the tissues of trees appears not to be a proven question; yet there seems to be evidence that at least a partial freezing of trees at temperatures not far below freezing occurs.

In a paper entitled, "The Maple Sap Flow,"* experiments on

*C. H. Jones, A. W. Edson and W. J. Morse, Vermont Agric. Exp. Sta., Bull. 103: 41–184. *pl.* 1–17 + *f.* 1–5. 1903.

tree temperatures are described and the following statement made: "Casual observations made by one of the writers in mid-winter, showed maples frozen for a depth of an inch and a half in one case, and an inch in another, while both white and yellow birches were

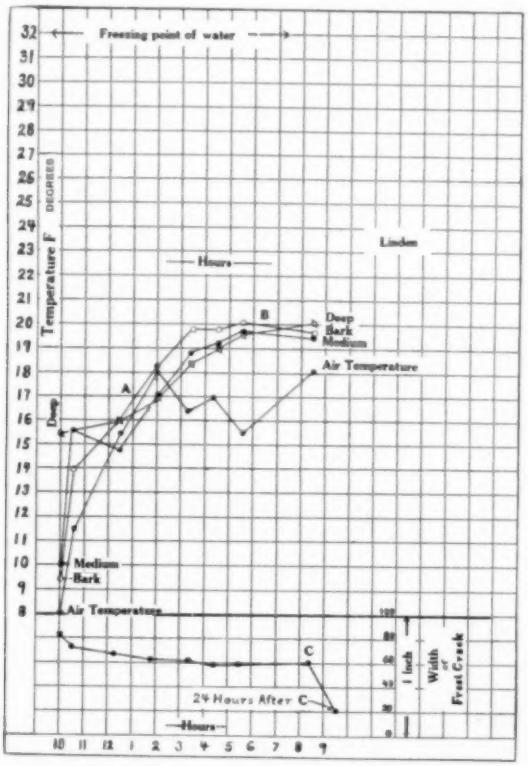

FIG. 18. Curves showing the change of width of frost crack in European linden and change of temperatures of the tree trunk and atmosphere. The bulb of the "Bark" thermometer was one inch below the surface; that of the "Medium" three inches below; that of the "Deep" five inches below. From *A* to *B* on the curves all three tree temperatures were the same. Yet the frost crack decreased in width with the general rise of temperature of the tree trunk. The mean at *A* was 15.4° F., and at *B* 19.6° F.

frozen through, except where the sun was beating upon them. It seems clear that some of the maple tissues are frozen in mid-winter." Also, as a summation, this view is given: "These data and observations lead to the conclusion that in the winter, the temperature of the maple tree tissues is generally below 0° C.

(32° F.), and that it may be considerably lower; that as the sugar season approaches it frequently rises above this point, and during its course is usually above, but occasionally falls below it; and that a part of the sap in the vessels of the outer rings freezes during the winter and may freeze during the sugar season."

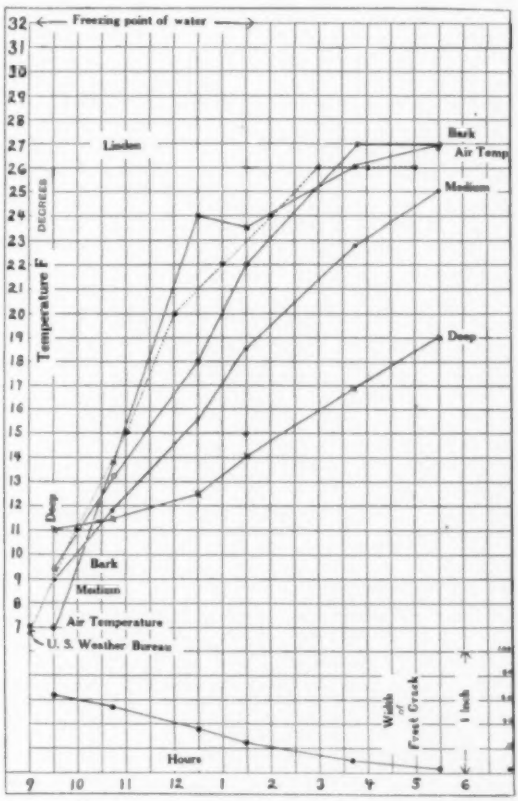

FIG. 19. Curves showing the change in width of frost crack and change of temperature of tree trunk and atmosphere. At *A* the tree trunk was at a uniform temperature to a depth of five inches. From this point on, the frost crack decreased in width consistently with the rise of temperature of the trunk of the tree. At *B*, where the thermometer readings showed the greatest difference of temperature between the successive layers of the tree trunk, the frost crack was nearly closed.

In experiments on certain plants evidence has been presented showing that freezing apparently is arrested by what appears to be a sub-cooling process; i. e., the confines of the liquid content

being so small as to prevent solidification. Consequently it is possible that under certain conditions sap does not freeze (even fractionally) until at least at a very low temperature, but the evidence of the thermometric movements of branches and the thermometric opening and closing of frost cracks indicate a change which begins at 32° F. and continues below that point, which must be regarded as evidence in favor of a fractional freezing of the sap. The alternative is that there is some cellular mechanism of the living wood of the tree which begins at 32° F. and continues as the temperature falls without the fractional freezing process, but parallel to such a change of state of the sap.

A considerable number of experiments were performed in order to ascertain, if possible, the coefficient of expansion of the tree trunk just below the bark. It was found that below freezing with the reduction of temperature a very large contraction occurred in the horizontal direction, transverse to the grain; on the other hand, that there was only a very small contraction in the longitudinal direction; also, that this contraction in the transverse direction was far greater than for a corresponding range above 32° F. Owing to a number of uncertainties in the experiments, they have not been published, and have been discarded for a more accurate method, which has been devised. The results indicated correspond with some measurements of Dr. J. G. Grossenbacher,* who measured the circumferences of a number of trees and determined that for a fall of temperature the decrease in circumference per degree was greater below freezing than above that point.

The fact, mentioned above, of greater coefficient of expansion below 32° in the transverse direction also corresponds with the published observation of Caspary who found that the circumference of the bark changed more rapidly than that of the wood cylinder in certain trees.†

GENERAL CONCLUSIONS

In this investigation the mechanics of the thermometric movements of branches has not yet been determined, but the

* Crown rot of fruit trees; field studies. New York State Agric. Exp. Sta. Tech. Bull. 23. 1912.

† R. Caspary, Neue Untersuchungen über Frostspalten. Bot. Zeit. 15: 329–35: 345–50; 361–71. 1857.

observations described have made an advance in the study of the subject. Some of the facts which have been determined are summarized below; temperatures are given in Fahrenheit for reasons previously stated.

1. The measurements which have been made on the movements of large branches of the European linden (*Tilia europaea*), due to a reduction of the atmospheric temperature seem to show that below 32° F. the movements are thermometric; when the temperature of the air falls below the freezing point of water (32° F.) (or very shortly above that point) the depression of the branches begins, and continues until at least 0° F., the lowest point at which observations were made.

2. There is scarcely any movement *above 32° F.*, the level of a branch at 70° F. being approximately the same as at 32° F. The freezing action of water (the aqueous part of a solution) is therefore the origin of the process which brings about the change in shape of the branch with change of temperature below 32° F. There seems, however, to be a very slight thermometric movement just above 32° F., the data on which is uncertain.

3. By making hourly observations not made hitherto, it has been shown that there may be a lag of one or two hours in the movements of the branches behind the changes of temperature, but if the air temperature is changing, a very slight change in the rate causes an almost immediate modification in the rate of movement of the branch. The observations made thus far indicate that a constant state of temperature for a considerable time, slightly below 32° F., causes a small movement; then the branch remains stationary until the temperature changes. These facts lead to the conclusion that the freezing liquid bringing about the thermometric movements of the branches below freezing temperatures is not pure water, but a solution, namely, the sap.

4. By artificially depressing the branches by means of weights, it was found that strains in the wood cause the branch to become temporarily depressed by a small amount. These strains in the branch, and the effect of lag of position of the branch behind the temperature of the air, explain the fact that in the curves showing the relation of the position of a branch to air temperatures the points are somewhat inconsistent.

5. The degree of moisture in the atmosphere, as shown by relative humidity observations, has apparently a negligible effect on the position of the branch.

6. Modulus of elasticity experiments seem to show that there is a stiffening in the branch below freezing (32° F.); but a stiffening of the branch should produce a less mobility or less depression of the branch whatever the stress; hence the slight effect observed due to a change in the bending constant of the branch arising from a reduction of temperature, taken alone, is in the opposite direction to the gross changes of the level of the branch observed at low temperatures.

7. Observations on frost cracks of the linden have shown that the width of the longitudinal cracks follow the changes in air temperature approximately below 32° F. When the crack first opens it is not thermometric because it is greatly affected by strain conditions, and resistance in the tearing of the wood.

Thermometers placed within the tree trunk at different distances from the surface indicated that the cracks were not caused by an unequal strain between the central core of the tree and the portion of the tree near the surface, arising directly from a difference of temperature, but due rather to excessive tension conditions in the living portion of the tree directly below the surface of the trunk.

All observations made indicate in a general way that the bending of the branches is closely related to the process which produced the longitudinal frost cracks in the linden.

8. Preliminary measurements indicate that the coefficient of expansion in the living linden in the transverse directions of the wood directly below the bark is very large below freezing, while small in the longitudinal direction.

9. Experiments on a *Paulownia* (*Paulownia tomentosa*) and a sycamore tree (*Platanus orientalis*), show scarcely a trace of the thermometric movement as exhibited by the linden.

The writer begs to acknowledge the courtesies shown by Professor Harper and other members of the Department of Botany at Columbia University, who have made many helpful suggestions pertaining to the botanical side of the present investigation.

PHOENIX PHYSICAL LABORATORY,
COLUMBIA UNIVERSITY

INDEX TO AMERICAN BOTANICAL LITERATURE

1916

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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